# 03\_mod\_approach

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[(#i\_mod\_2flankspim)=](#_Toc173424235)

[(#i\_mod\_rem)=](#_Toc173424236)

[(#i\_mod\_rest)=](#_Toc173424237)

[(#i\_mod\_tifc)=](#_Toc173424238)

[(#i\_mod\_ds)=](#_Toc173424239)

[(#i\_mod\_tte)=](#_Toc173424240)

[(#i\_mod\_ste)=](#_Toc173424241)

[(#i\_mod\_ste\_tte\_is)=](#_Toc173424242)

[(#i\_mod\_is)=](#_Toc173424243)

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[Spatial mark-resight (SMR) (type of SCR model)](#_Toc173424254)

[Spatial count (SC) / Unmarked spatial capture-recapture (type of SCR model)](#_Toc173424255)

[Spatial Partial Identity Model (Categorical SPIM; catSPIM)](#_Toc173424256)

[Spatial Partial Identity Model (2-flank SPIM)](#_Toc173424257)

[Random encounter models (REM)](#_Toc173424258)

[Random encounter and staying time (REST)](#_Toc173424259)

[Time in front of the camera (TIFC)](#_Toc173424260)

[Distance sampling (DS)](#_Toc173424261)

[Time-to-event (TTE) model](#_Toc173424262)

[Space-to-event (STE) models](#_Toc173424263)

[Instantaneous sampling (IS)](#_Toc173424264)

[Behaviour](#_Toc173424265)

# DEMO

## (#i\_mod\_inventory)=\*\*\*\*\*\*

# Species inventory

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| **\*\*{{ term\_mod\_inventory }}\*\*:** {{ term\_def\_mod\_inventory }} | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| **Advanced - How the Model Works** | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
| * No formal [assumptions](#mods\_modelling\_assumption) {{Wearn & Glover-Kapfer, 2017}} | | Maximum flexibility for [study](#survey) design (e.g., [camera days per camera location](#camera\_days\_per\_camera\_location) or use of [lure](#baitlure\_lure) {{Rovero et al., 2013; Wearn & Glover-Kapfer, 2017}} | | | Not reliable estimates for inference ("considered as unfinished, working drafts"){{Wearn & Glover-Kapfer, 2017}} | |
| **Figures & Videos** | | | | | | |
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| **Analytical tools & resources** | | | | | | |
| **Name** | **Link** | | **Reference** | | | **Additional\_info** |
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| **References** | | | | | | |

## (#i\_mod\_divers\_rich)=\*\*\*

# Species diversity & richness

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| \*\*{{ term\_mod\_divers\_rich }}\*\*: {{ term\_def\_mod\_divers\_rich }} | | | | | | |
| **Overview - How the Model Works**  “Species richness” can be thought of as the sum of different species seen in a particular area during a particular time period.  as “species diversity”  The simplest way to understand the different between | | | | | | |
| **Advanced - How the Model Works**  Parameters:   * **α-richness (alpha richness):** species richness at the level of an individual camera location * **γ-richness (gamma richness):** species richness across a whole study area * **β-diversity (betadiversity)**: the differences between the communities or, more formally, the variance among the communities   Observed *v.s* estimated species richness   * **Observed species richness**: the sum of the number of species seen (e.g. Kitamura et al. 2010; Pettorelli et al. 2010; Ahumada et al. 2011; Samejima et al. 2012)   + Observed species richness will not, in general, be a reliable index of actual species richness because, even if sampling effort is strictly controlled, the detectability of species will vary across samples * **Estimated species richness** (e.g. Tobler et al. 2008; Kinnaird & O’Brien 2012; Brodie et al. 2015; Yue et al. 2015; Wearn et al. 2016)   + Species richness estimation involves attempting to correct for “imperfect detection”, i.e. the fact that some species in a given sample may have been missed (Box 6-1).   A black and white image of different types of objects  Description automatically generated  ```{figure} ../03\_images/Pyron\_2010\_Fig1.png  ---  align: center  height: 150px  name: directive-fig  ---  (Pyron et al., 2010)  ```  The two principal ways of estimating species richness from camera trap data are with:   * non-parametric estimators {{Gotelli & Chao 2013}}, which use information about the rarest species in the sample to provide a minimum estimate of the number of true species (e.g. {{Tobler et al. 2008}}), * or 2) occupancy models {{MacKenzie et al. 2006}} | | | | | | |
| **Assumptions** | | **Pros** | | | | **Cons** |
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| **Figures & Videos** | | | | | | |
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| **Analytical tools & resources** | | | | | | |
| **Name** | **Link** | | **Reference** | | **Additional\_info** | |
| Chapter 9 Community composition | https://bookdown.org/c\_w\_beirne/wildCo-Data-Analysis/composition.html#estimated-richnes | |  | |  | |
| R package “vegan” | https://cran.r-project.org/web/packages/vegan/index.html | |  | |  | |
| EstimateS | https://www.robertkcolwell.org/pages/1407 | |  | |  | |
| **References**  (Iknayan et al., 2014)  (Gotelli & Colwell, 2010)  (Gotelli & Colwell, 2001)  (Pyron, 2010)  (Tobler et al. 2008)  (Kinnaird & O’Brien 2012)  (Brodie et al. 2015)  (Yue et al. 2015)  (Wearn et al. 2016)  (Kitamura et al. 2010)  (Pettorelli et al. 2010)  (Ahumada et al. 2011)  (Samejima et al. 2012) | | | | | | |

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

# Relative abundance indices

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| **Relative abundance indices:** An index of relative abundance. When observational data is converted to a detection rate (i.e., the frequency [count] of independent detections of a species within a distinct time period). An index can be a count of animals or any sign that is expected to vary with population size (Caughley, 1977; O'Brien, 2011). | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| **Advanced - How the Model Works**  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,  A black and white math equation  Description automatically generated  ```{figure} ./03\_images/Clarke-et-al\_2023\_eqn\_rai1.png  :align: center  ```  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:  A black and white symbol  Description automatically generated  ```{figure} ./03\_images/Clarke-et-al\_2023\_eqn\_rai2.png  :align: center  ```  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. | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
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| **Figures & Videos** | | | | | | |
| Engineering Proceedings | Free Full-Text | Modelling of Leishmaniasis  Infection Dynamics: A Comparative Time Series Analysis with VAR, VECM,  Generalized Linear and Markov Switching Models  https://www.mdpi.com/2673-4591/39/1/38 | | | | TheWorldOfZeroInflatedModels | | |
| A diagram of a diagram  Description automatically generated  Modified from Gilbert et al., 2021  ```{figure} ./03\_images/Gilbert-et-al\_2019\_Fig3.png  :align: center  ``` | | | |  | | |
| **Analytical tools & resources** | | | | | | |
| **Name** | **URL** | | **Note** | | | **Reference** |
| Probabilistic gaps | <https://mabecker89.github.io/abmi.camera.extras/articles/gaps.html> | | - | | |  |
| Introduction to Camera Trap Data Management and Analysis in R > Chapter 12 Activity | <https://bookdown.org/c\_w\_beirne/wildCo-Data-Analysis/activity.html> | | - | | |  |
| R package “activity” | <https://cran.r-project.org/web/packages/activity/index.html> | | - | | |  |
| R package “overlap” | <https://cran.r-project.org/web/packages/overlap/index.html> | | - | | |  |
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| **References**  {{ ref\_intext\_clarke-et-al\_2023 }} | | | | | | |

## 

## (#i\_mod\_behaviour)=

# Behaviour (Diel activity patterns, mating, boldness, etc.)

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| **Overview - How the Model Works** | | | | | |
| **Advanced - How the Model Works** | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** |
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| **Simulations and Field Experiments {{ ref\_intext\_clarke-et-al\_2023 }}** | | | | | |
| **Figures & Videos** | | | | | |
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| **Analytical tools & resources** | | | | | |
| **Name** | **Link** | | **Reference** | **Additional\_info** | |
| Paper - A model-based hypothesis framework to define and estimate the diel niche via the ‘Diel.Niche’ R package | <https://www.biorxiv.org/content/10.1101/2023.06.21.545898v1> | |  | “An R package to evaluate hypotheses of diel phenotypes based on empirical data and estimate the probabilitiy of activity during the crepuscular, daytime, and nighttime periods.” | |
| R package - [Diel-Niche-Modeling](https://github.com/diel-project/Diel-Niche-Modeling) | <https://github.com/diel-project/Diel-Niche-Modeling> | |  |
| R Shiny - Diel.Niche Shinyapp | <https://shiny.celsrs.uri.edu/bgerber/DielNiche/> | |  |
| An Introduction to Camera Trap Data Management and Analysis in R > Chapter 14 Behavior | <https://bookdown.org/c\_w\_beirne/wildCo-Data-Analysis/behavior.html> | |  |  | |
|  |  | |  |  | |
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| **References**  (Caravaggi et al., 2017) | | | | | |

**notes**

--- (Wearn & Glover-Kapfer, 2017)---

* The focus of the study could be on a particular location (such as a lekking site or a fruiting tree) or on a particular species. However, as for the study types we have considered above, the starting point is to establish what the key assumptions of the modelling are, and then design the sampling appropriately with this in mind.
* For example, imagine you are interested in the rate at which a given behaviour occurs in a species (e.g. vigilance: Schuttler et al. 2017), and how this differs across major habitat types in your study area. If your aim was to make inferences about the population in your study area as a whole, then you would want to take a representative sample of individuals, and you would want to observe them at random locations and random times of the day. All of this could be achieved using random sampling points, stratified by habitat type, with camera traps set to trigger throughout the 24 hr period. Cameras would ideally be sufficiently spaced apart to obtain samples from lots of different individuals (e.g. 1 km apart, depending on the species). Similarly, the number of sampling points, and how long each is sampled for, would have to be sufficient in order to obtain a reasonable number of behavioural observations in each habitat type (> 20 per stratum would be a sensible minimum target). The length of the study would ideally not be too long, for example restricted to a single season, so as to provide a snapshot of the prevalence of the behaviour in different habitat types in the absence of any temporal trends in the behaviour (temporal or seasonal trends could be a focus of follow-up surveys). This basic approach to sampling design for a behavioural study would be suitable for the study of activity patterns, which is a common use of camera traps. In this case, some aspects of sample size have been investigated (Ridout & Linkie 2009; Rowcliffe et al. 2014). This work suggests that a sample size of 20-25 observations will offer useful insights into activity patterns over a 24 hr period, but that larger samples (> 100) will be needed to characterise the activity patterns with any reasonable level of precision, especially if the pattern has a complicated shape (Ridout & Linkie 2009; Rowcliffe et al. 2014).
* species interactions and niche partitioning via comparisons of co-occurrence and activity patterns (de Almeida Jacomo et al. 2004; Kukielka et al. 2013; Farris et al. 2014; Wang et al. 2015; Bu et al. 2016; Cusack et al. 2016; Sweitzer and Furnas 2016).

# 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** | | | | |
|  | | | Gilbert-et-al\_2019\_Fig3.png | |
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| **Analytical tools & resources** | | | | |
| **Name** | **Link** | **Reference** | | **Additional\_info** |
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| **References**  (Alberta Remote Camera Steering Committee (RCSC) et al., 2023)  {{ ref\_intext\_clarke-et-al\_2023 }} | | | | |

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

# Poisson model

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| **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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**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** | | | | | | |
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**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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| **References** | | | | | | |

**notes**

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

# Hurdle model

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| **Hurdle model (Mullahy,1986; Heilbron 1994):** A regression model used in the setting of excess zeros (zero-inflation) and overdispersion (Mullahy, 1986). Hurdle models (aka "zero-altered" models) differ from zero-inflation models in that they are two-part models, and the zero and non-zero counts are modelling separately (thus, they are only adequate when the counting process cannot generate a zero value) (Blasco-Moreno et al., 2019). [relative abundance indices] | | | | | | |
| **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 | | |
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| **Analytical tools & resources** | | | | | | |
| Name | **Link** | | **Reference** | | | **Additional\_info** |
| 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 |
| R package countreg (Zeileis et al., 2008) | <https://rdrr.io/rforge/countreg/>  <https://rdrr.io/rforge/countreg/f/inst/doc/countreg.pdf>  https://www.zeileis.org/papers/Kleiber+Zeileis-2016.pdf | |  | | | 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}

## (#i\_mod\_cr\_cmr)=

# Capture-recapture (CR) / Capture-mark-recapture (CMR)

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| **Capture-recapture (CR) model / Capture-mark-recapture (CMR) model (Karanth, 1995; Karanth & Nichols, 1998):** A method of estimating the abundance or density of marked populations using the number of animals detected and the likelihood animals will be detected (detection probability). CR (Karanth, 1995; Karanth & Nichols, 1998) can be used to estimate vital rates where all newly detected unmarked animals become marked and are distinguishable in future (Efford, 2022). Spatially explicit capture-recapture (SECR; Borchers & Efford, 2008; Efford, 2004; Royle & Young, 2008) models have largely replaced CR and CMR models and provide more accurate density estimates (Blanc et al., 2013, Obbard et al., 2010, Sollmann et al., 2011). | | | | | |
| **Overview - How the Model Works** | | | | | |
| 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 ≠ 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:  A number of letters and numbers  Description automatically generated with medium confidence  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:  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 adhoc 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).  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). | | | | | |
| **Assumptions** | | **Pros** | | **Cons** | |
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| **Simulations and Field Experiments {{ ref\_intext\_clarke-et-al\_2023 }}** | | | | | |
| **Figures & Videos** | | | | | |
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| **References** | | | | | |

**notes**

## (#i\_mod\_scr\_secr)=

# Spatial capture-recapture (SCR) / Spatially explicit capture recapture (SECR)

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| Spatially explicit capture-recapture (SECR) / Spatial capture-recapture (SCR) (Borchers & Efford, 2008; Efford, 2004; Royle & Young, 2008; Royle et al., 2009): The SECR (or SCR) method is used to estimate the density of marked populations; an extension of traditional capture-recapture (CR; Karanth, 1995; Karanth & Nichols, 1998) models (Karanth, 1995; Karanth & Nichols, 1998) that explicitly accounts for camera location and animal movement (Burgar et al., 2018). SECR models use spatially Referenced individual capture histories to infer where animals' home range centres are, assuming that detection probability decreases with increasing distance between cameras and home range centres {{ ref\_intext\_clarke-et-al\_2023 }}. SECR models can be implemented using different statistical frameworks, including Bayesian estimation (Royle and Young, 2008; Morin et al., 2022). | | | |
| **Overview - How the Model Works** | | | |
| **Advanced - How the Model Works {{ ref\_intext\_clarke-et-al\_2023 }}**  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:    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).    Diagram of a diagram of activity model  Description automatically generated  ```{figure} ./03\_images/image\_files/clarke-et-al\_2023\_fig4\_clipped.png  :name: \*\*Clarke et al., 2023 - 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.  :align: center  ```  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 cameratrap-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), dataaugmented maximum likelihood estimation (Royle et al. 2014), and data-augmented Bayesian estimation (Royle and Young 2008; Morin et al. 2022).  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.  A diagram of a graph and a diagram of a graph  Description automatically generated  ```{figure} ./03\_images/clarke\_et\_al\_2023/clarke-et-al\_2023\_fig5\_clipped.png  :align: center  ```  \*\*Clarke et al., 2023 - 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). | | | |
| **Figures & Videos** | | | |
| A black and red dotted pattern  Description automatically generated with medium confidence  Figure 1: Hypothetical Poisson distribution of range centres near an array of detectors. We estimate the intensity (density) of this distribution.  ```{figure} ./03\_images/  :align: center  ```  Efford, M. (2011). secr—Spatially explicit capture–recapture in R. | | **Video:** [PAWS: Spatial Capture Recapture Data Analysis Part 1](https://www.youtube.com/watch?v=aTbk-jWyMcU) https://www.youtube.com/watch?v=aTbk-jWyMcU | |
| **Video:** [PAWS: Spatial Capture Recapture Data Analysis Part 2](https://www.youtube.com/watch?v=IHVez1a_hqg) https://www.youtube.com/watch?v=IHVez1a\_hqg | | **Video:** [J. Andrew Royle,"Spatial Capture-Recapture Modeling"](https://www.youtube.com/watch?v=4HKFimATq9E)  https://www.youtube.com/watch?v=4HKFimATq9E | |
| **Analytical tools & resources** | | | |
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| Article - Fast Evaluation of Study Designs for Spatially Explicit Capture–Recapture (Efford & Boulanger, 2019). | <<https://doi.org/10.1111/2041-210X.13239>> | - |  |
| **References**  {{ ref\_bibtext\_clarke-et-al\_2023 }} | | | |  |  | {{ ref\_bibtext\_efford-boulanger\_2019 }} |

## (#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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| **Spatial mark-resight (SMR) (Chandler & Royle, 2013; Sollmann et al., 2013a, 2013b):** A method used to estimate the density of "partially marked populations by combining... [detection] histories of marked [individuals] and counts of unmarked [individuals]" (Doran-Myers, 2018) over several occasions (Sollman et al., 2013a; Rich et al., 2014; Whittington et al., 2018). SMR models can be implemented using different statistical frameworks, including Bayesian estimation (Royle and Young, 2008; Morin et al., 2022). | | | | | |
| **Overview - How the Model Works** | | | | | |
| **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:  A mathematical equation with black letters  Description automatically generated  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 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** | |
|  | |  | |  | |
| **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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**notes**

## (#i\_mod\_sc)=

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

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| **Spatial count (SC) model / Unmarked spatial capture-recapture (Chandler & Royle, 2013):** A method used to estimate the density of unmarked populations; similar to SECR (Borchers & Efford, 2008; Efford, 2004; Royle & Young, 2008; Royle et al., 2009); however, SC models account for individuals' unknown identities using the spatial pattern of detections (Chandler & Royle, 2013; Sun et al., 2022). SC uses trap-specific counts to estimate the location and number of activity centres to estimate density. | | | | | |
| **Overview - How the Model Works** | | | | | |
| Advanced - 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 trapspecific 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:  A black and white math equation  Description automatically generated  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).  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  where 𝑀 ≫ 𝑁 and 𝜔𝑖 is the probability of existence of individual 𝑖 within population 𝑁 (Chandler and 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 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** | | **Pros** | | **Cons** | |
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| **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 (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. | | | | | |
| **Figures & Videos** | | | | | |
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| **Analytical tools & resources** | | | | | |
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| SC models with the ‘nimble’ package (de Valpine et al., 2017 |  | |  | |  |
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| **References**  {{ ref\_intext\_clarke-et-al\_2023 }} | | | | | |

**notes**

## (#i\_mod\_catspim)=

# Categorical partial identity model (catSPIM) (Augustine et al., 2019; Sun et al., 2022)

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| **Categorical partial identity model (catSPIM) (Augustine et al., 2019; Sun et al., 2022):** A method used to estimate the density of partially marked populations in which the "spatial locations of where partial identity samples are captured to probabilistically resolve their complete identities" (Augustine et al., 2018, 2019). catSPIM models use partial identity traits (e.g., sex class, antler points) to help infer individual identities (Augustine et al., 2019; Sun et al., 2022). catSPIM is an extension of the SC model (Chandler & Royle, 2013). | | | | | | |
| **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. | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
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| **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. | | | | | | |
| **Figures & Videos** | | | | | | |
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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 |
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| **References**  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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| **Spatial partial identity model (2-flank SPIM) (Augustine et al., 2018):** A method used to estimate the density of partially marked populations in which the “spatial locations of where partial identity samples are captured to probabilistically resolve their complete identities” (Augustine et al., 2018). Paired sampling design is commonly used to capture both the right and left flanks of an animal to resolve individual identities (Augustine et al., 2018). 2-flank SPIM is an extension of the SCR model (Borchers & Efford, 2008; Efford, 2004; Royle & Young, 2008; Royle et al., 2009). | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| **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\_rem)=

# Random encounter model (REM)

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| **Random encounter model (REM) (Rowcliffe et al., 2008, 2013):** A method used to estimate the density of unmarked populations; uses the rate of independent captures, an estimate of movement rate, average group size, and the area sampled by the remote camera. | | | | | |
| **Overview - How the Model Works** | | | | | |
| **Advanced - How the Model Works {{ ref\_intext\_clarke-et-al\_2023 }}**  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:  A math equation with black text  Description automatically generated  ```{figure} ./03\_images/Clarke-et-al\_2023\_eqn\_rem1.png  :align: center  ```  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).  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).  A diagram of a cone with a person walking  Description automatically generated  ```{figure} ./03\_images/clarke\_et\_al\_2023/Clarke-et-al\_2023\_Fig2\_clipped.png  :align: center  ```  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). | | | | | |
| **Assumptions** | | **Pros** | | **Cons** | |
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| **Simulations and Field Experiments {{ ref\_intext\_clarke-et-al\_2023 }}**  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 capturerecapture (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, livetrapping 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 censusderived 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). | | | | | |
| **Figures & Videos** | | | | | |
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**notes**

* Palencia et al., 2023 - Accordingly, to obtain a CV lower than 0.20, required for effective wildlife management Palencia (Williams et al., 2002), the effort with REM will be around 100 camera traps.
* Accordingly, to obtain a CV lower than 0.20, required for effective wildlife management (Williams et al., 2002), the effort with REM will be around 100 camera traps. Regarding CT-DS, Bessone et al. (2020) obtained an average CV of 0.37 in spite of sampling 750 locations.
* In this respect, Capelle et al. (2021) concluded that a wide variety of survey designs can be applied to achieve CV between 0.10 and 0.20 with CT-DS, for instance, with at least 100 sampling days at as few 50 camera trap placements.

## (#i\_mod\_rest)=

# Random encounter and staying time (REST)

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| **Random encounter and staying time (REST) model (Nakashima et al., 2017):** A recent modification of the REM (Nakashima et al., 2017) that substitutes staying time (i.e., the cumulative time in the cameras' detection zone) for movement speed (staying time and movement speed are inversely proportional) (Cappelle et al., 2021). | | | | | |
| **Overview - How the Model Works**   * “The REST model describes the relationship among population density, mean number of detections by a camera trap during a survey period, and staying time of individual animals in a predetermined detection zone in which individuals are certain to be detected by the camera trap.” (Nakashima et al., 2017). | | | | | |
| **Advanced - How the Model Works {{ ref\_intext\_clarke-et-al\_2023 }}**  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:    ```{figure} ./03\_images/clarke\_et\_al\_2023/Clarke-et-al\_2023\_eqn\_rest1.png  :align: center  ```  where 𝑌is 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 measured from the moment an animal’s hind leg enters the focal area until it exits (i.e., 𝑇𝑒𝑥𝑖𝑡 − 𝑇𝑒𝑛𝑡𝑒𝑟).  Importantly, estimates of density 𝐷 must be corrected for activity level – that is, the proportion of time animals are active – such that:    ```{figure} ./03\_images/clarke\_et\_al\_2023/Clarke-et-al\_2023\_eqn\_rest2.png  :align: center  ```  where 𝐷̂ 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).  A fox in the woods  Description automatically generated  ```{figure} ./03\_images/clarke\_et\_al\_2023/Clarke-et-al\_2023\_Fig8\_clipped.png  :align: center  ```  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. | | | | | |
| **Assumptions** | | **Pros** | | **Cons** | |
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| **Simulations and Field Experiments {{ ref\_intext\_clarke-et-al\_2023 }}**  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 km2 in Garland et al. (2020) and 10 individuals per km2 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 livetrapping 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-toEvent 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 km2; 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/km2); 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). | | | | | |
| **Figures & Videos** | | | | | |
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**notes**

* UBC\_CAMERA\_Report1\_Density\_31Jan2023.pdf
* Garland et al. (2020) advise that the REST model should not be used for species that exhibit heterogeneous patterns of moving and resting.

## (#i\_mod\_tifc)=

# Time in front of the camera (TIFC)

[refer to [RC Study Design Decision Support Tool](https://ualbertaca-my.sharepoint.com/:f:/g/personal/cjsteven_ualberta_ca/Er14FQ50a0pPnmEAox7MRu8BI6rFhKGF-6ykeZjnEoG8lg?e=mvTICq) > ModApproach\_TIFC]

## (#i\_mod\_ds)=

# Distance sampling (DS)

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| **Distance sampling (DS) model (Howe et al., 2017):** A method to estimate abundance by using distances at which animals are detected (from survey lines or points) to model abundance as a function of decreasing detection probability with animal distance from the camera (using a decay function) (Cappelle et al., 2021; Howe et al., 2017). | | | | | |
| **Overview - How the Model Works** | | | | | |
| **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; 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).  A graph of a number of data  Description automatically generated  ```{figure} ./03\_images/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 (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 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:    ```{figure} ./03\_images/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 (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  ```{figure} ./03\_images/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/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 (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, 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/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 (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:  A black and white image of a mathematical equation  Description automatically generated  ```{figure} ./03\_images/clarke\_et\_al\_2023/Clarke-et-al\_2023\_eqn\_ds4.png  :align: center  ```  where 𝐷𝐶 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** | | **Pros** | | **Cons** | |
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| **Simulations and 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/km2 and 6.25 camera traps/km2 (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 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; Twining et al. 2022). While all methods produced densities within accepted ranges, DS tended to underestimate density (Twining et al. 2022). | | | | | |
| **Figures & Videos** | | | | | |
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| **Analytical tools & resources** | | | | | |
| **Name** | **Link** | | **Reference** | | **Additional\_info** |
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| **References**  {{ ref\_intext\_clarke-et-al\_2023 }} | | | | | |

**notes**

## (#i\_mod\_tte)=

# Time-to-event (TTE)

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| **Time-to-event (TTE) model (Moeller et al., 2018):** A method used to estimate abundance or density from the detection rate while accounting for animal movement rates (Moeller et al., 2018). The TTE model assumes perfect detection (though there is a model extension to account for imperfect detection that requires further testing). | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| **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 (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:  A black and white math equation  Description automatically generated with medium confidence  ```{figure} ./03\_images/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:  A mathematical equation with numbers  Description automatically generated  ```{figure} ./03\_images/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 (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).  A screenshot of a computer  Description automatically generated  ```{figure} ./03\_images/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 (Moeller et al. 2018). Thus, practitioners need measures of animal movement speed. | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
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| **Simulations and Field Experiments {{ ref\_intext\_clarke-et-al\_2023 }}**  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). | | | | | | |
| **Figures & Videos** | | | | | | |
| ```{figure} ./03\_images/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 |
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| **References**  {{ ref\_intext\_clarke-et-al\_2023 }} | | | | | | |

**notes**

## (#i\_mod\_ste)=

# Space-to-event (STE)

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| **Space-to-event (STE) model (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) (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 (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.  A forest with mossy ground  Description automatically generated  ```{figure} ./03\_images/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 (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 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 (Moeller et al. 2018).  A black background with a white arrow  Description automatically generated  ```{figure} ./03\_images/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/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 (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). | | | | | | |
| **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 (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). 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*; 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 markrecapture. | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
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| **Figures & Videos** | | | | | | |
| A screenshot of a screen  Description automatically generated  ```{figure} ./03\_images/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**

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 (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

* 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) (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 (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 (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:    ```{figure} ./03\_images/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 (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 (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). | | | | | |
| **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 | | (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 | | (Palencia et al., 2021) | | Burst inconstistency record |
|  |  | |  | |  |
|  |  | |  | |  |
| **References**  {{ ref\_intext\_clarke-et-al\_2023 }} | | | | | |

**notes**

# Assumptions, Pros, Cons

## changes here will reflect in books above

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| --- | --- | --- | --- | --- |
| **Objective** | **Approach** | **Assumptions** | **Pros** | **Cons** |
| [Species inventory](#mods_inventory) | [Species inventory](#mods_inventory) | * No formal [assumption](#mods_modelling_assumption)s {{Wearn & Glover-Kapfer, 2017}} | * Maximum flexibility for [study](#survey) design (e.g., [camera days per camera location](#camera_days_per_camera_location) or use of [lure](#baitlure_lure) {{Rovero et al., 2013}}){{Wearn & Glover-Kapfer, 2017}} | * Not reliable estimates for inference ("considered as unfinished, working drafts"){{Wearn & Glover-Kapfer, 2017}} |
| Species richness | Species richness | * [Camera location](#camera_location)s are [randomly placed](#sampledesign_random){{Wearn & Glover-Kapfer, 2017}} * [Camera location](#camera_location)s are independent{{Wearn & Glover-Kapfer, 2017}} * [Detection probability](#detection_probability) of different species remains the same1 ("true" species richness estimation involves attempting to correct for "[imperfect detection](#imperfect_detection)"{{Wearn & Glover-Kapfer, 2017}}) * Sampling effort is comparable between [camera location](#camera_location)s {{Royle & Nichols, 2003}} | * Fundamental to ecological theory and often a key metric used in management{{Wearn & Glover-Kapfer, 2017}} * Simple to analyze, interpret and communicate{{Wearn & Glover-Kapfer, 2017}} * Models exist to estimate asymptotic species richness, including unseen species (simple versions of these models - "EstimateS" and the "vegan" R-packages){{Wearn & Glover-Kapfer, 2017}} | * Dependent on the scale (as captured in the species-area relationship){{Wearn & Glover-Kapfer, 2017}} * All species have equal weight in calculations, and community evenness is disregarded{{Wearn & Glover-Kapfer, 2017}} * Insensitive to changes in abundance, community structure and community composition{{Wearn & Glover-Kapfer, 2017}} |
| Species diversity | Species diversity | * [Camera location](#camera_location)s are [randomly placed](#sampledesign_random){{Wearn & Glover-Kapfer, 2017}}) * [Camera location](#camera_location)s are independent {{Wearn & Glover-Kapfer, 2017}}) * [Detection probability](#detection_probability) of different species remains the same{{Wearn & Glover-Kapfer, 2017}}) | * Captures evenness and richness (although some indices only reflect evenness) {{Wearn & Glover-Kapfer, 2017}} * Most indices are easy to calculate and widely implemented in software packages (e.g., "EstimateS" and "vegan" in R){{Wearn & Glover-Kapfer, 2017}} | * Many indices exist, and it can be difficult to choose the most appropriate {{Wearn & Glover-Kapfer, 2017}} * Comparing measures across space, time and studies can be very difficult {{Wearn & Glover-Kapfer, 2017}} * Insensitive to changes in community composition {{Wearn & Glover-Kapfer, 2017}} (however, this may be conditional on study design) |
| Species diversity | β-diversity | * [Camera location](#camera_location)s are [randomly placed](#sampledesign_random) {{Wearn & Glover-Kapfer, 2017}} * Randomness and independence{{Wearn & Glover-Kapfer, 2017}} * Samples are assumed to have been taken at random from the broader population of sites{{Wearn & Glover-Kapfer, 2017}} | * Can be used to track changes in community composition {{Wearn & Glover-Kapfer, 2017}} * Plays a critical role in effective conservation prioritization (e.g., designing reserve networks) {{Wearn & Glover-Kapfer, 2017}} * Important for detecting changes in the fundamental processes{{Wearn & Glover-Kapfer, 2017}} | * No single best measure for all purposes {{Wearn & Glover-Kapfer, 2017}} * Interpretation/communication not always straightforward {{Wearn & Glover-Kapfer, 2017}} * Scale-dependent (i.e., influenced by the size of the communities that are being included) {{Wearn & Glover-Kapfer, 2017}} |
| [Occupancy](#occupancy) | [Occupancy models](#mods_occupancy){{MacKenzie et al., 2002}} | * [Occupancy](#occupancy) is constant {{MacKenzie et al., 2002}} (abundance is constant) {{MacKenzie et al., 2006}} * [Camera location](#camera_location)s are independent{{MacKenzie et al., 2006}} * Detections are [independent](#independent_detections) {{MacKenzie et al., 2006}} * The probability of [occupancy](#occupancy) and detection are constant across all [camera location](#camera_location)s within a stratum or can be modelled using covariates {{MacKenzie et al., 2006}} * Species are not misidentified{{MacKenzie et al., 2006}} | * Does not require individual identification {{MacKenzie et al., 2006}} * Only requires detection/non-detection data for each site {{Wearn & Glover-Kapfer, 2017}} * Relatively easy-to-use software exists for fitting models (PRESENCE, MARK, and the "unmarked" R package){{Wearn & Glover-Kapfer, 2017}} * "Open" models exist that allow for the estimation of site colonization and extinction rates{{MacKenzie et al., 2006; Wearn & Glover-Kapfer, 2017}} * Multi-species [occupancy models](#mods_occupancy) {{MacKenzie et al., 2002}} allow the inclusion of interactions among species while controlling for [imperfect detection](#imperfect_detection){{Wearn & Glover-Kapfer, 2017}} | * [Occupancy](#occupancy) {{MacKenzie et al., 2002}} only measures distribution; it may be a misleading indicator of changes in abundance{{Wearn & Glover-Kapfer, 2017}} * Interpretation/communication of results may not be straightforward (if the scale of movement is much larger than the [camera spacing](#camera_spacing) the results should be interpreted as "probability of use" rather than [occupancy](#occupancy)){{Wearn & Glover-Kapfer, 2017}} |
| [Relative abundance indices](#mods_relative_abundance) | [Poisson](#mods_poisson) | * Many [assumption](#mods_modelling_assumption)s exist(since used for many approaches){{Wearn & Glover-Kapfer, 2017}} | * Simple to calculate and technically possible (even with small sample sizes when robust methods might fail){{Wearn & Glover-Kapfer, 2017}} * [Relative abundance indices](#mods_relative_abundance) often do correlate with abundance{{Wearn & Glover-Kapfer, 2017}} * Calibration with independent [density](#density) estimates is possible{{Wearn & Glover-Kapfer, 2017}} | * Difficult to draw inferences (a large number of [assumptions](#mods_modelling_assumption)); comparisons across space, time, species, and studies are difficult{{Wearn & Glover-Kapfer, 2017}} * Requires stringent [study design](#survey) (e.g., random sampling, standardized methods){{Wearn & Glover-Kapfer, 2017}} * Detection rates from remote cameras cannot be used as an index to compare relative abundance across species {{Rowcliffe & Carbone, 2008}} |
|  | [Zero-inflated Poisson (ZIP)](#Mods_zip) {{Lambert, 1992}} |  |  |  |
|  | [Negative binomial (NB)](#mods_negative_binomial){{Mullahy, 1986}} |  |  |  |
|  | [Zero-inflated negative binomial (ZINB)](#mods_zinb){{McCullagh & Nelder, 1989}} |  |  |  |
|  | [Hurdle models](#mods_hurdle) {{Mullahy, 1986; Heilbron 1994}} |  |  |  |
|  | Other |  |  |  |
|  |  |  |  |  |
| Population size / Absolute abundance / vital rates / [Density](#density); [Marked population](#typeid_marked) | [Capture-recapture (CR) / capture-mark-recapture (CMR)](#mods\_cr\_cmr) {{Karanth, 1995; Karanth & Nichols, 1998}} | * Demographic closure (i.e., no births or deaths) {{Wearn & Glover-Kapfer, 2017}} * Geographic closure (i.e., no immigration or emigration) {{Wearn & Glover-Kapfer, 2017}} * All individuals have at least some probability of being detected {{Rovero et al., 2013}} * Sampled area encompasses the full extent of individuals’ movements {{Karanth & Nichols, 1998; Rovero et al., 2013}} * Activity centres are randomly dispersed {{Clarke et al., 2023}} * Activity centres are stationary {{Clarke et al., 2023}} | * May be used as a [relative abundance index](#mods_relative_abundance) that controls for [imperfect detection](#imperfect_detection) {{Wearn & Glover-Kapfer, 2017}} * Easy-to-use software exists to implement (e.g., CAPTURE); MARK Implements more complicated models with covariates (and must be used for [mark-resight modelling](#mods_mr)) {{Wearn & Glover-Kapfer, 2017}} * Can use the robust design with "open" models to obtain recruitment and survival rate estimates {{Wearn & Glover-Kapfer, 2017}} | * Requires that individuals are distinguishable. {{Wearn & Glover-Kapfer, 2017}} However, CR {{Karanth, 1995; Karanth & Nichols, 1998}} has also been used to estimate abundance of species that lack natural markers but that have phenotypic and/or environment-induced characteristics {{Noss et al., 2003; Kelly et al., 2008; Rovero et al., 2013}} * When the sample size is large enough to reliably estimate [density](#density) with CR, {{Karanth, 1995; Karanth & Nichols, 1998}} individuals are unlikely to have a unique marker {{Noss et al., 2003; Kelly et al., 2008; Rovero et al., 2013}} * Dependent on the surveyed area, which is difficult to track and calculate {{Wearn & Glover-Kapfer, 2017}} * Requires a minimum number of captures and recaptures {{Wearn & Glover-Kapfer, 2017}} * Relatively stringent requirements for [study design](#survey) (e.g., no "holes" in the trapping grid) {{Wearn & Glover-Kapfer, 2017}} * Geographic closure at the plot level, which is often unrealistic {{Wearn & Glover-Kapfer, 2017}} * Assumes a specific relationship between abundance and detection {{Wearn & Glover-Kapfer, 2017}}  * [Density](#density) cannot be explicitly estimated because the true area animals occupy is never measured (only approximated) {{Chandler & Royle, 2013}} |
| [Density](#density) / population size; [Marked population](#typeid_marked) | [Spatially explicit capture recapture (SECR)](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} (also referred to as [Spatial capture-recapture [SCR])](#mods_scr_secr) | * Demographic closure (i.e., no births or deaths) {{Wearn & Glover-Kapfer, 2017}}  * [Detection probability](#detection_probability) of different individuals is equal {{Wearn & Glover-Kapfer, 2017}}   + or, for SECR, individuals have equal [detection probability](#detection_probability) at a given distance from the centre of their home range {{Wearn & Glover-Kapfer, 2017}} * Detections of different individuals are [independent](#independent_detections) {{Wearn & Glover-Kapfer, 2017}} * Behaviour is unaffected by cameras and marking {{Wearn & Glover-Kapfer, 2017}} * Individuals do not lose marks {{Wearn & Glover-Kapfer, 2017}} * Individuals are not misidentified {{Wearn & Glover-Kapfer, 2017}} * Surveys are independent {{Wearn & Glover-Kapfer, 2017}} * For conventional models, geographic closure (i.e., no immigration or emigration) {{Wearn & Glover-Kapfer, 2017}} * Spatially explicit models have further [assumption](#mods_modelling_assumption)s about animal movement {{Wearn & Glover-Kapfer, 2017; Rowcliffe et al., 2008; Royle et al., 2009; O’Brien et al., 2011}}; these include:   + Home ranges are stable {{Wearn & Glover-Kapfer, 2017}}   + Movement is unaffected by cameras {{Wearn & Glover-Kapfer, 2017}}  * + [Camera location](#camera_location)s are [randomly placed](#sampledesign_random) with respect to the distribution and orientation of home ranges {{Wearn & Glover-Kapfer, 2017}}   + Distribution of home range centres follows a defined distribution ([Poisson](#mods_poisson), or other, e.g.,negative binomial) {{Wearn & Glover-Kapfer, 2017}} | * Produces direct estimates of [density](#density) or population size for explicit spatial regions {{Chandler & Royle, 2013}} * Allows researchers to mark a subset of the population/to take advantage of natural markings {{Wearn & Glover-Kapfer, 2017}} * Estimates are fully comparable across space, time, species and studies {{Wearn & Glover-Kapfer, 2017}} * [Density](#density) estimates obtained in a single model, fully incorporate spatial information of locations and individuals {{Wearn & Glover-Kapfer, 2017}} * Both likelihood-based and Bayesian versions of the model have been implemented in relatively easy-to-use software (DENSITY and SPACECAP, respectively, as well as associated R packages) {{Wearn & Glover-Kapfer, 2017}} * Flexibility in [study](#survey) design (e.g., "holes" in the trapping grid) {{Wearn & Glover-Kapfer, 2017}} * "Open" [SECR](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} models exist that allow for estimation of recruitment and survival rates {{Wearn & Glover-Kapfer, 2017}} * "Avoid ad-hoc definitions of [study area](#study_area) and edge effects" {{Doran-Myers, 2018}}  * [SECR](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} accounts for variation in individual [detection probability](#detection_probability); can produce spatial variation in [density](#density); [SECR](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} more sensitive "to detect moderate-to-major populations changes" (+/-20-80%) {{Morin et al., 2022; Clarke et al., 2023}} | * Requires that individuals are identifiable {{Wearn & Glover-Kapfer, 2017}} * Requires that a minimum number of individuals are trapped (each recaptured multiple times ideally) {{Wearn & Glover-Kapfer, 2017}} * Requires that each individual is captured at a number of [camera locations](#camera_location) {{Wearn & Glover-Kapfer, 2017}} * Multiple cameras per station may be required to identify individuals; difficult to implement at large spatial scales as it requires a high density of cameras {{Morin et al., 2022; Clarke et al., 2023}} * May not be precise enough for long-term monitoring {{Green et al., 2020}} * Cameras must be close enough that animals are detected at multiple [camera location](#camera_location)s {{Wearn & Glover-Kapfer, 2017}} (may be challenging to implement at large scales as many cameras are needed)" {{Chandler & Royle, 2013}} * ½ MMDM (Mean Maximum Distance Moved) will usually lead to an underestimation of home range size and thus overestimation of [density](#density) {{Parmenter et al., 2003; Noss et al., 2012; Wearn & Glover-Kapfer, 2017}} |
| [Density](#density); [Marked population](#typeid_marked) | [Spatial mark-resight (SMR)](#mods_smr) (type of SCR model) {{Chandler & Royle, 2013; Sollmann et al., 2013a; Sollmann et al., 2013b}} | * Demographic closure (i.e., no births or deaths) {{Chandler & Royle, 2013; Clarke et al., 2023}} * Geographic closure (i.e., no immigration or emigration) {{Chandler & Royle, 2013; Clarke et al., 2023}} * Individuals do not lose marks {{Wearn & Glover-Kapfer, 2017}} (for maximum precision), but [SMR](#mods_smr) {{Chandler & Royle, 2013; Sollmann et al., 2013a; Sollmann et al., 2013b}} does allow for inclusion of [marked](#typeid_marked) but unidentified resighting detections {{Sollmann et al., 2013b; Rich et al., 2014}} * Individuals are not misidentified {{Wearn & Glover-Kapfer, 2017}} * Failure to identify marked individuals is random {{Whittington et al., 2018; Clarke et al., 2023}}  * [Marked animals](#typeid_marked) are a random sample of the population with home ranges located inside the state space {{Sollmann et al., 2013a; Rich et al., 2014}} * Detections are [independent](#independent_detections) {{Chandler & Royle, 2013; Clarke et al., 2023}} * Individuals have equal [detection probability](#detection_probability) at a given distance from the centre of their home range {{Wearn & Glover-Kapfer, 2017}} * Detections of different individuals are [independent](#independent_detections) {{Wearn & Glover-Kapfer, 2017}} * Movement is unaffected by cameras {{Wearn & Glover-Kapfer, 2017}} * Behaviour is unaffected by cameras and marking {{Wearn & Glover-Kapfer, 2017}}  * [Camera location](#camera_location)s are [randomly placed](#sampledesign_random) relative to the distribution and orientation of home ranges {{Wearn & Glover-Kapfer, 2017}}  * [Camera location](#camera_location)s are close enough together that animals are detected at multiple cameras {{Chandler & Royle, 2013; Clarke et al., 2023}} * Surveys are independent {{Wearn & Glover-Kapfer, 2017}} * Home ranges are stable {{Wearn & Glover-Kapfer, 2017}} * Distribution of home range centres follows a defined distribution ([Poisson](#mods_poisson), or other, e.g.,negative binomial) {{Wearn & Glover-Kapfer, 2017}} * Animals’ activity centres are randomly dispersed {{Chandler & Royle, 2013; Clarke et al., 2023}} * Animals’ activity centres are stationary {{Chandler & Royle, 2013; Clarke et al., 2023}} * All animals have stable activity centres within home ranges where detection probability is greatest {{Royle & Nichols, 2003; Sollmann et al., 2013a; Whittington et al., 2018}} | * Estimates are fully comparable to [SECR](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} of [marked](#typeid_marked) species {{Wearn & Glover-Kapfer, 2017}} * Can be applied to a broader range of species than [SECR](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} {{Wearn & Glover-Kapfer, 2017}} * Allows researcher to take advantage of natural markings {{Wearn & Glover-Kapfer, 2017}} * Allows researcher to mark a subset of the population (note - precision is dependent on number of [marked](#typeid_marked) individuals in a population) {{Wearn & Glover-Kapfer, 2017}} | * Animals may have to be physically captured and [marked](#typeid_marked) if natural marks do not exist on enough individuals {{Wearn & Glover-Kapfer, 2017}} * All individuals must be identifiable {{Wearn & Glover-Kapfer, 2017}} * Allows for [density](#density) estimation for a [unmarked population](#typeid_unmarked), but the precision of the [density](#density) estimates are likely to be very low value {{Wearn & Glover-Kapfer, 2017}} * Remains poorly tested with camera data, although it offers promise {{Wearn & Glover-Kapfer, 2017}}  * [Density](#density) estimates are likely less precise than with [SECR](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} or [REM](#mods_rem), unless a large proportion of the population have marks {{Wearn & Glover-Kapfer, 2017}} * Requires sampling points to be close enough that individuals encounter multiple cameras {{Wearn & Glover-Kapfer, 2017}} |
| [Density](#density); [Unmarked population](#typeid_unmarked) | [Spatial count (SC)](#mods_sc) / Unmarked spatial capture-recapture (type of SCR model) {{Chandler & Royle, 2013; Royle et al., 2014}} | * [Camera location](#camera_location)s are close enough together that animals are detected at multiple cameras {{Chandler & Royle, 2013; Clarke et al., 2023}} * Demographic closure (i.e., no births or deaths) {{Chandler & Royle, 2013; Clarke et al., 2023}} * Geographic closure (i.e., no immigration or emigration) {{Chandler & Royle, 2013; Clarke et al., 2023}} * Detections are [independent](#independent_detections) {{Chandler & Royle, 2013; Clarke et al., 2023}} * Animals’ activity centres are randomly dispersed {{Chandler & Royle, 2013; Clarke et al., 2023}} * Animals’ activity centres are stationary {{Chandler & Royle, 2013; Clarke et al., 2023}} | * Does not require individual identification {{Clarke et al., 2023}} | * Produces imprecise estimates even under ideal circumstances unless supplemented with auxiliary data (e.g., telemetry) {{Doran-Myers, 2018; Chandler & Royle, 2013; Sollmann et al., 2013a; Sollmann et al., 2013b}} * Precision decreases with an increasing number of individuals detected at a camera" {{Morin et al., 2022}} (as overlap of individuals’ home ranges increases) {{Augustine et al., 2019; Clarke et al., 2023}} * Not appropriate for low [density](#density) or elusive species when recaptures too few to confidently infer the number and location of activity centres" {{Clarke et al., 2023; Burgar et al., 2018}} * Not appropriate for high-[density](#density) populations with evenly spaced activity centres (camera[-specific] counts will be too similar and impair activity centre inference)" {{Clarke et al., 2023}} * Ill-suited to populations that exhibit group-travelling behaviour" {{Sun et al., 2022; Clarke et al., 2023}} * Study design (camera arrangement) can dramatically affect the accuracy and precision of [density](#density) estimates" {{Clarke et al., 2023; Sollmann, 2018}} * Cameras must be close enough that animals are detected at multiple [camera location](#camera_location)s (may be challenging at large scales as many cameras are needed)" {{Chandler & Royle, 2013; Clarke et al., 2023}} |
| [Density](#density) / population size; [Partially Marked population](#typeid_partially_marked) | [Spatial Partial Identity Model (Categorical SPIM; catSPIM)](#mods_catspim) {{Augustine et al., 2019; Sun et al., 2022}}  (Extension of [SC](#mods_sc) model using animal traits (e.g., [Sex Class](#sex_class), antler points) and model parameters) | * Same as [SC](#mods_sc) {{Augustine et al., 2019; Sun et al., 2022; Clarke et al., 2023}}   + Camera must be close enough together that animals are detected at multiple cameras {{Chandler & Royle, 2013; Clarke et al., 2023}}   + Demographic closure (i.e., no births or deaths) {{Chandler & Royle, 2013; Clarke et al., 2023}}   + Geographic closure (i.e., no immigration or emigration) {{Chandler & Royle, 2013; Clarke et al., 2023}}   + Detections are independent {{Chandler & Royle, 2013; Clarke et al., 2023}} * Activity centres are randomly dispersed {{Chandler & Royle, 2013; Clarke et al., 2023}} * Activity centres are stationary {{Chandler & Royle, 2013; Clarke et al., 2023}} * Each categorical identifier (e.g., male/female, collared/not collared, etc) has fixed number of possibilities {{Sun et al., 2022}} * All possible values of categorical identifiers occur in the population with probabilities that can be estimated {{Augustine et al., 2019; Sun et al., 2022; Clarke et al., 2023}} * Every individual is assigned "full categorical identity" (i.e., "set of traits given all categorical identifiers and possibilities") {{Augustine et al., 2019; Clarke et al., 2023}} * Individuals' identifying traits do not change during the survey (e.g., antlers present/absent) {{Augustine et al., 2019}} | * May produce more precise and less biased [density](#density) estimates than [SC](#mods_sc) with less information {{Sun et al., 2022; Clarke et al., 2023}} | * Sensitive to non-independent movement (e.g., group-travel; can cause over-dispersion and bias estimates {{Sun et al., 2022; Clarke et al., 2023}}); may limit application to solitary species only {{Sun et al., 2022; Clarke et al., 2023}} * May produce be less reliable/accurate estimates for high-[density](#density) populations {{Sun et al., 2022; Clarke et al., 2023}} * Too few categorical identifiers/ possibilities can result in mis-assignments and overestimating [density](#density) {{Augustine et al., 2019; Parmenter et al., 2003; Clarke et al., 2023}} |
| [Density](#density) / population size; [Partially Marked population](#typeid_partially_marked) | [Spatial Partial Identity Model (2-flank SPIM](#mods_2flankspim)[)](#mods_2flankspim) {{Augustine et al., 2018}} (extension of [SCR](#mods_scr_secr) model augmented with data from partially-identifying images) | * Same as [SCR](#mods_scr_secr) {{Augustine et al., 2018; Clarke et al., 2023}} * Capture processes for left-side, right-side and both-side images are independent {{Augustine et al., 2018; Clarke et al., 2023}} | * Same as [SCR](#mods_scr_secr) {{Augustine et al., 2018; Clarke et al., 2023}} * Improved precision of [density](#density) estimates relative to [SCR](#mods_scr_secr) {{Augustine et al., 2018; Davis et al., 2021; Clarke et al., 2023}} * Many study designs can be used ([paired](#sampledesign_paired) [sample stations](#sample_station), single [camera location](#camera_location)s, and hybrids of both [paired](#sampledesign_paired)- and single [camera location](#camera_location)s {{Augustine et al., 2018; Davis et al., 2021; Clarke et al., 2023}} * Can be used with single-camera and hybrid sampling designs, and therefore requires fewer cameras (or sample more area) than [SCR](#mods_scr_secr) {{Augustine et al., 2018; Clarke et al., 2023}} * May be more robust to non-independence than [SC](#mods_sc) {{Augustine et al., 2018; Clarke et al., 2023}} | * Computationally intensive {{Augustine et al., 2018; Clarke et al., 2023}} * Increased precision is less pronounced in high-[density](#density) populations {{Augustine et al., 2018; Clarke et al., 2023}} |
| [Density](#density); [Unmarked](#typeid_unmarked) | [Random encounter models (REM)](#mods_rem) {{Rowcliffe et al., 2008; Rowcliffe et al., 2013}}> | * Demographic closure {{Rowcliffe et al., 2008; Doran-Myers, 2018}}(i.e., no births or deaths) * Geographic closure {{Rowcliffe et al., 2008; Doran-Myers, 2018}}(i.e., no immigration or emigration)  * [Camera location](#camera_location)s are [random](#sampledesign_random)ly placed relative to animal movement {{Wearn & Glover-Kapfer, 2017; Rowcliffe et al., 2008}} * Animal movement is unaffected by the cameras {{Wearn & Glover-Kapfer, 2017; Rowcliffe et al., 2008}} * Accurate counts of independent "contacts" [camera location](#camera_location)s {{Wearn & Glover-Kapfer, 2017; Rowcliffe et al., 2008}} * Unbiased estimates of animal activity levels and speed {{Rowcliffe et al., 2014; Rowcliffe et al., 2016; Wearn & Glover-Kapfer, 2017}} * Camera’s [detection zone](#detection_zone) can be approximated well using a 2D cone shape, defined by the radius and angle parameters {{Rowcliffe et al., 2011}} * If activity and speed are to be estimated from camera data, two additional [assumption](#mods_modelling_assumption)s: * All animals are active during the peak daily activity {{Rowcliffe et al., 2014}} * Animals moving quickly past a camera are not missed {{Rowcliffe et al., 2016}} | * Flexible study design (e.g., "holes" in grids allowed, [camera spacing](#camera_spacing) less important) {{Wearn & Glover-Kapfer, 2017}} * Can be applied to [unmarked](#typeid_unmarked) species {{Wearn & Glover-Kapfer, 2017}} * Allows community-wide [density](#density) estimation {{Wearn & Glover-Kapfer, 2017}} * Outputs also include informative parameter estimates (i.e., animal speed and activity levels, and [detection zone](#detection_zone) parameters) {{Wearn & Glover-Kapfer, 2017}} * Comparable estimates to [SECR](#mods_scr_secr)[ {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}}] {{Wearn & Glover-Kapfer, 2017}} * Does not require [marked animals](#typeid_marked) or identification of individuals {{Rowcliffe et al., 2008; Doran-Myers, 2018}} * Can use [camera spacing](#camera_spacing) without regard to population home range size {{Rowcliffe et al., 2008; Doran-Myers, 2018}} * Direct estimation of [density](#density); avoids ad-hoc definitions of [study area](#study_area) {{Rowcliffe et al., 2008}} | * Requires relatively stringent study design, particularly (e.g., random sampling and use of [bait](#baitlure_bait) or [lure](#baitlure_lure)) {{Wearn & Glover-Kapfer, 2017}} * Requires independent estimates of animal speed or measurement of animal speed within videos {{Wearn & Glover-Kapfer, 2017}} * No dedicated, simple software {{Wearn & Glover-Kapfer, 2017}} * Random relative to animal movement, grid preferred, avoid multiple captures of same individual, area coverage important for abundance estimation {{Rovero et al., 2013}} * Possible sources of error include inaccurate measurement of [detection zone](#detection_zone) and movement rate {{Rowcliffe et al., 2013; Cusack et al., 2015}} |
| [Density](#density); [Unmarked](#typeid_unmarked) | [Random encounter and staying time (REST)](#mods_rest) {{Nakashima et al., 2018}} | * Demographic closure (i.e., no births or deaths) and geographic closure (i.e., no immigration or emigration) (animal [density](#density) is constant during the [survey](#survey)) {{Rowcliffe et al., 2008}} * Detection is perfect {{Wearn & Glover-Kapfer, 2017}} ([detection probability](#detection_probability) "p" = 1) unless otherwise modelled {{Nakashima et al., 2018}}  * [Camera location](#camera_location)s are representative of the available habitat {{Nakashima et al., 2018}}  * [Camera location](#camera_location)s are [random](#sampledesign_random)ly placed relative to the spatial distribution of animals {{Nakashima et al., 2018}} * Animal movement and behaviour are not affected by cameras {{Nakashima et al., 2018}} * Detections are [independent](#independent_detections) {{Nakashima et al., 2018}} * The observed distribution of staying time in the focal area fits the distribution of movement {{Nakashima et al., 2018}} * The observed staying time must follow a given parametric distribution {{Nakashima et al., 2018}} | * Provides unbiased estimates of animal [density](#density), even when animal movement speed varies, and animals travel in pairs {{Nakashima et al., 2018}} | * Attraction or aversion to cameras is exhibited in some species {{Meek et al., 2016}} and could affect the time within the [detection zone](#detection_zone) and subsequently affect estimates of [density](#density) {{Doran-Myers, 2018}} * Requires accurate measurements of the area of the camera [detection zone](#detection_zone), which has been a challenge in previous studies {{Rowcliffe et al., 2011; Cusack et al., 2015; Anile & Devillard, 2016; Doran-Myers, 2018; Nakashima et al., 2018}} * Mathematically challenging {{Cusack et al., 2015}} |
| [Density](#density); [Unmarked](#typeid_unmarked) | [Time in front of the camera (TIFC)](#mods_tifc) {{Huggard, 2018; Warbington & Boyce, 2020; Becker et al., 2022}} | * [Camera location](#camera_location)s are [random](#sampledesign_random)ly placed or representative relative to animal movement {{Becker et al., 2022}} * Movement is unaffected by the cameras {{Becker et al., 2022}} * Reliable detection of animals in part of the camera’s [FOV](#field_of_view) (at least) {{Becker et al., 2022}} | * Does not require individual identification {{Warbington & Boyce, 2020}} * Makes no [assumption](#mods_modelling_assumption) about home range {{Warbington & Boyce, 2020}} * Comparable to estimates from [SECR](#mods_scr_secr) {{Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008; Royle et al., 2009}} {{Warbington & Boyce, 2020}} | * Requires careful calculation of the effective area of detection {{Warbington & Boyce, 2020}} * A high level of measurement error {{Becker et al., 2022}} |
| [Density](#density); [Unmarked](#typeid_unmarked) | [Distance sampling (DS)](#mods_distance_sampling) {{Borchers & Marques, 2017; Howe et al., 2017}} | * [Random](#sampledesign_random) or [systematic random](#sampledesign_systematic_random) placements (consistent with the [assumption](#mods_modelling_assumption) that points are placed independently of animal locations) {{Howe et al., 2017}}  * [Camera location](#camera_location)s are [random](#sampledesign_random)ly placed relative to animal movement {{Palencia et al., 2021}} * Detection is perfect ([detection probability](#detection_probability) "p" = 1) at focal area / distance 0 {{Palencia et al., 2021}} * Demographic closure (i.e., no births or deaths) and geographic closure (i.e., no immigration or emigration) (animal [density](#density) is constant during the [survey](#survey)) {{Palencia et al., 2021}} * Animal movement and behaviour are unaffected by the cameras {{Palencia et al., 2021}} * Animals are detected at initial locations (e.g., they do not change course in response to the camera prior to detection) {{Palencia et al., 2021}} * Distances are measured exactly (however if the data from different distances will be grouped ("binned") for analysis later, an accuracy of +/- 1m may suffice) {{Palencia et al., 2021}} * Detections are [independent](#independent_detections) {{Palencia et al., 2021}} * Snapshot moments selected independently of animal locations {{Palencia et al., 2021}} | * A shortcut to controlling for variation in [detection distances](#detection_distance) by only counting individuals within a short distance with an unobstructed view, and well sampled across cameras and species {{Wearn & Glover-Kapfer, 2017}}  * [Density](#density) estimates are unbiased by animal movement "since camera-animal distance is measured at a certain instant in time (intervals of duration *\*t\** apart)" {{Howe et al., 2017; Clarke et al., 2023}} * Can be applied to low-[density](#density) populations {{Howe et al., 2017; Clarke et al., 2023}} * Does not require individual identification {{Howe et al., 2017}} | * May require discarding a portion of the dataset (when the best fitting model truncates the dataset) {{Wearn & Glover-Kapfer, 2017}} * Biased by movement speed {{Palencia et al., 2021}} * Best suited to larger animals; the smaller the focal species, the lower remote cameras must be set, which reduces the depth of the [viewshed](#fov_viewshed), and thus sampling size and the flexibility of the model" {{Howe et al., 2017; Clarke et al., 2023}} * Does not permit inference about spatial variation in abundance (unless using hierarchical distance which can model spatial variation as a function of covariates) {{Gilbert et al., 2021; Clarke et al., 2023}} * "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 process)" {{Clarke et al., 2023}} * Requires a good understanding of the focal populations’ activity patterns; [density](#density) estimates can be biased (e.g., under-estimated) when regular periods of inactivity are not accounted for (using detection times to infer periods of activity may help overcome this limitation)" {{Howe et al., 2017; Palencia et al., 2021; Clarke et al., 2023}} * Tends to underestimate [density](#density) {{Howe et al., 2017; Twining et al., 2022; Clarke et al., 2023}} * Low population [density](#density) and reactivity to cameras may be major sources of bias" {{Bessone et al., 2020; Clarke et al., 2023}} |
| [Density](#density); [Unmarked](#typeid_unmarked) | [Time-to-event (TTE) model](#mods_tte) {{Moeller et al., 2018}} | * Demographic closure (i.e., no births or deaths) {{Moeller et al., 2018; Loonam et al., 2021}} * Geographic closure (i.e., no immigration or emigration) at the level of the sampling frame (area of interest); this assumption does not apply at the plot-level (area sampled by the camera) {{Moeller et al., 2018; Loonam et al., 2021}} * Animal movement and behaviour are unaffected by the cameras {{Palencia et al., 2021}}  * [Camera location](#camera_location)s placement is [random](#sampledesign_random), [systematic](#sampledesign_systematic), or [systematic random](#sampledesign_systematic_random) {{Moeller et al., 2018}} * Detections are [independent](#independent_detections) {{Moeller et al., 2018}} * Spatial counts of animals (or counts in equal subsets of the landscape) are Poisson-distributed {{Loonam et al., 2021}} * Accurate estimate of movement speed {{Loonam et al., 2021}} * Detection is perfect ([detection probability](#detection_probability) "*\*p\**" = 1) {{Moeller et al., 2018}} | * Can be efficient for estimating abundance of common species (with a lot of images) {{Moeller et al., 2018}} | * Requires independent estimates of movement rate (difficult to obtain without telemetry data) {{Moeller et al., 2018}} * Assumes that [detection probability](#detection_probability) is 1 (or apply extension to account for [imperfect detection](#imperfect_detection)) {{Moeller et al., 2018}} |
| [Density](#density); [Unmarked](#typeid_unmarked) | [Space-to-event (STE)](mods_ste) models {{Moeller et al., 2018}} | * Demographic closure (i.e., no births or deaths) {{Moeller et al., 2018}} * Geographic closure (i.e., no immigration or emigration) {{Moeller et al., 2018}}  * [Camera location](#camera_location)s are [random](#sampledesign_random)ly placed {{Moeller et al., 2018}} * Detections are [independent](#independent_detections) {{Moeller et al., 2018}} * Spatial counts of animals in a small area (or counts in equal subsets of the landscape) are Poisson-distributed {{Loonam et al., 2021}} * Detection is perfect ([detection probability](#detection_probability) "*\*p\**" = 1) {{Moeller et al., 2018}} | * Can be efficient for estimating abundance of common species (with a lot of images) {{Moeller et al., 2018}} * Does not require estimate of movement rate {{Moeller et al., 2018}} | * Assumes that [detection probability](#detection_probability) is 1 {{Moeller et al., 2018}} |
| [Density](#density); [Unmarked](#typeid_unmarked) | [Instantaneous sampling (IS)](#mods_instantaneous_sampling) {{Moeller et al., 2018}} | * Demographic closure (i.e., no births or deaths) {{Moeller et al., 2018}} * Geographic closure (i.e., no immigration or emigration) {{Moeller et al., 2018}}  * [Camera location](#camera_location)s are [random](#sampledesign_random)ly placed {{Moeller et al., 2018}} * Detections are [independent](#independent_detections) {{Moeller et al., 2018}} * Detection is perfect ([detection probability](#detection_probability) "*\*p\**" = 1) {{Moeller et al., 2018}} | * Can be efficient for estimating abundance of common species (with a lot of images) {{Moeller et al., 2018}} * Flexible [assumption](#mods_modelling_assumption) of animals’ distribution {{Moeller et al., 2018}} | * Requires accurate counts of animals {{Moeller et al., 2018}} * Assumes that perfect ([detection probability](#detection_probability) "*\*p\**" = 1) {{Moeller et al., 2018}} * Reduced precision {{Moeller et al., 2018}} |
| Behaviour | Behaviour | * [Assumption](#mods_modelling_assumption)s vary depending on the behavioural metric {{Wearn & Glover-Kapfer, 2017}} * For studies of activity patterns and temporal interactions of species: activity level is the only factor determining [detection rates](#detection_rate); animals are active when camera [detection rate](#detection_rate) reaches its maximum in daily cycle {{Royle et al., 2014; Rovero & Zimmerman, 2016}} | * Can detect difficult to observe behaviours (i.e., boldness, or mating) {{Bridges & Noss, 2011}} * Long-term data on behavioural changes that would be difficult to obtain otherwise (i.e., time-limited human observers, or costly GPS collars) {{Bridges & Noss, 2011}} * Can monitor behaviour in response to specific locations (i.e., compost sites, which might be more difficult using GPS collars for example) {{Rovero & Zimmerman, 2016}} * Can evaluate interactions between species {{Rovero & Zimmerman, 2016}} | * Behavioural metrics may not reflect the behavioural state (inferred) {{Rovero & Zimmerman, 2016}} * Biases associated with equipment (i.e., presence of the camera itself may change behaviour studied) {{Rovero & Zimmerman, 2016}} * Difficult to consider individual variation {{Rovero & Zimmerman, 2016}} |