Camera trap monitoring of unmarked animals: a map of the relationships between population size estimators

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Abstract

The use of camera traps to monitor unmarked animal populations has expanded during the last decade, leading to the development of several density estimation methods. This plethora of methods may be confusing for the newcomer to the field. Some methods, such as the random encounter model, require the knowledge of the mean travel speed of the animals, while others, such as camera trap distance sampling, do not rely on such assumptions. Different methods, like instantaneous sampling, camera trap distance sampling, and the association model, rely on similar types of data, but do not seem identical. In this article, I explore the relationships between different density estimators, including the random encounter model, the random encounter and staying time model, the time-to-event model, camera-trap distance sampling, the association model, and the space-to-event model. I show how these different estimators are related under two simplifying assumptions (perfect detectability, and animal movements following the ideal gas model). I develop a map of mathematical relationships between these estimators, which can help newcomers to understand how these methods are interconnected.

Keywords: random encounter models, random encounter and staying time, instantaneous sampling, time-to-event model, space-to-event model, camera-trap distance sampling

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Introduction

Many methods have been developed in the last two decades to estimate the size of a population of unmarked animals using camera traps (Gilbert et al., 2020; Wearn et al., 2022). Two main families of methods have been proposed: methods relying on animal-traps encounters and methods relying on animal-traps associations.

Animal-traps encounters can be defined as to the full passage of an animal through the field of view of a camera trap. Each encounter is defined in time: it is characterised by a starting time, an ending time, a duration, a path length. These characteristics can be measured using traps equipped with movement sensors. Numerous population size estimators rely on the number of encounters detected by the traps. This is for example the case of the random encounter model, one of the first methods proposed to estimate unmarked population size with camera trap data (Rowcliffe et al., 2008). The main challenge of encounter-based methods is that more active animals generate more encounters with traps, so that the unbiased estimation of population size requires the knowledge of the mean travel speed of animals – the so-called day range. Several methods have been proposed to estimate this day range using data collected on animal-traps encounters (e.g. Palencia et al., 2021, 2019). The alternative random encounter and staying time model uses the encounters duration measured by the traps to implicitly account for the mean travel speed of animals (Nakashima et al., 2017).

In contrast, methods relying on animal-trap associations do not require the explicit or implicit use of this day range to estimate population density. An animal-trap association is defined as the instantaneous presence of an animal in the field of view of a camera trap. Associations typically arise from time-lapse programming, where camera-traps capture images at regular time steps. The number of associations at a given time and place corresponds to the number of animals detected in a single image frame captured by a trap. The total number of associations in the field of view of all camera traps at a given time is, on average, proportional to the population density. Several methods, such as the instantaneous sampling (Moeller et al., 2018), the association model (Campos-Candela et al., 2018), or the camera-trap distance sampling (Howe et al., 2017), rely on this relationship.

Moeller et al. (2018) proposed two additional methods that, while not directly relying on the number of associations or encounters, still leverage these concepts. The time-to-event approach relies on encounters: it uses the time elapsed between the start of a sampling period and the first encounter detection to estimate population density (the longer this duration, and the lower the density). The space-to-event approach, on the other hand, relies on associations detected using time-lapse programming. It estimates population size by sequentially sampling traps at a given time until an association is detected, using the cumulative area of the sampled traps to estimate population density (the larger this area, and the lower the density).

This plethora of estimation methods may be confusing for newcomers to this field. In this paper, I present a map of the relationships between the different estimators discussed above (Fig. 1). My aim is to demonstrate the mathematical similarities between the different estimators under the assumptions of perfect detectability and of animals moving according to the ideal gas model used by Rowcliffe et al. (2008). This provides an intuitive understanding of how these methods are interconnected. To keep the paper as concise as possible, I have included the mathematical developments in the appendix.

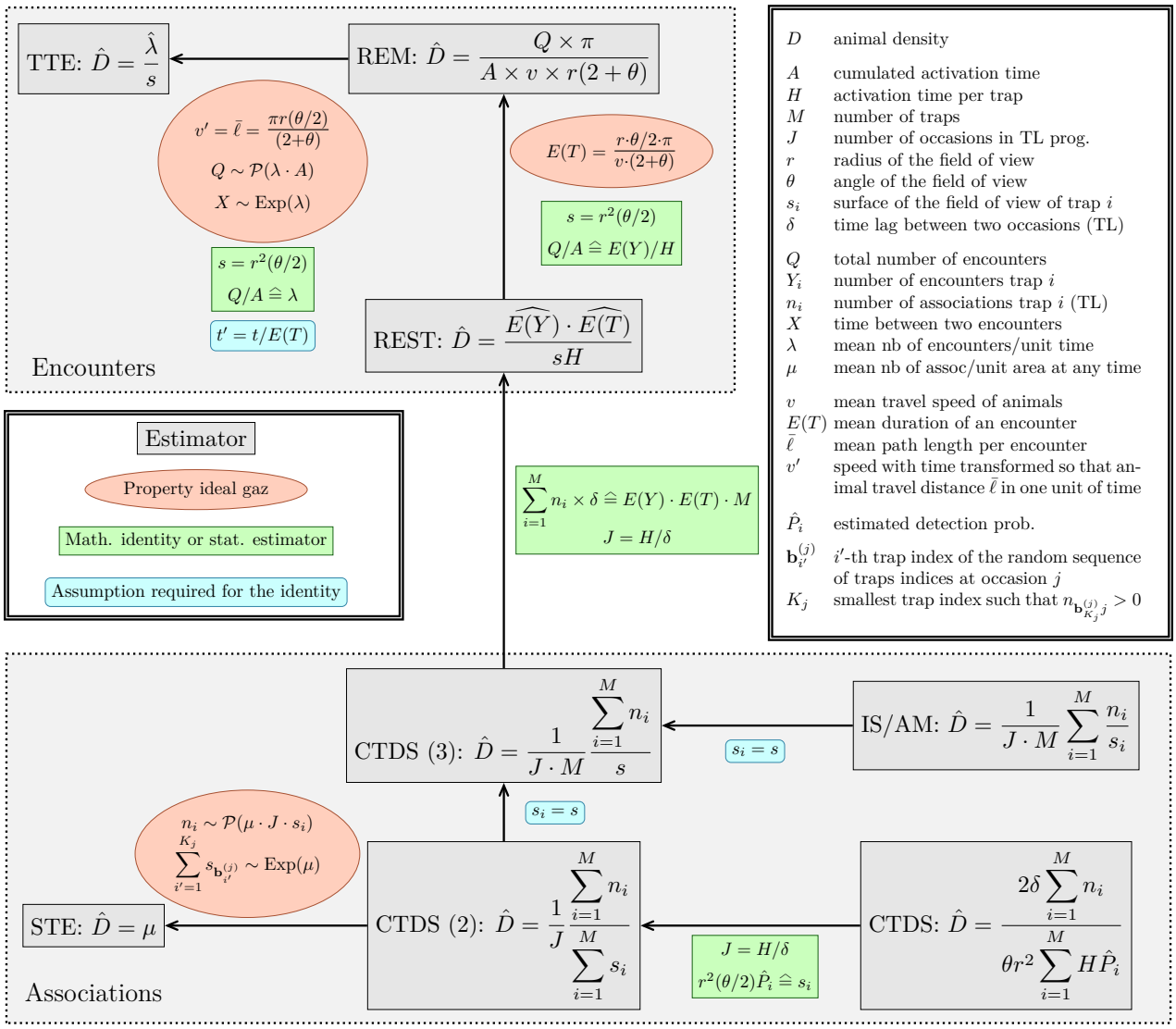

Figure 1 – Map of the mathematical relationships between different density estimators based on the camera trap monitoring of a population of unmarked animals. Each grey square corresponds to an estimator (REM = random encounter model, REST = random encounter and staying time, TTE = time-to-event model, CTDS = camera-trap distance sampling, IS/AM = instantaneous sampling/association model, STE = space-to-event model). We distinguish association-based methods and encounter-based methods. For each pair of estimators, we indicate close to the arrow the conditions under which the two estimators are identical. We distinguish the properties of the ideal gas model, the mathematical identities/statistical estimators ($\mathrel{\widehat{=}}$ means that the right-hand side can be estimated by the left-hand side), and the assumptions required for the identity to hold. The inset at the top-right gives the meaning of the mathematical notations.

Understanding the map

General methodology

In this paper, I study the relationships between the population size estimators corresponding to the 7 following methods: the random encounter model (REM), the random encounter and staying time model (REST), the time-to-event model (TTE), the space-to-event model (STE), the

instantaneous sampling approach (IS), the association model (AM), and camera-trap distance sampling (CTDS).

One difficulty is that these estimators were developed in different statistical contexts, focusing on different aspects of the density estimation. Thus, some approaches take place in a modelling framework with a density estimated using the maximum likelihood (e.g. REST, TTE, STE, AM), making distributional assumptions on the data collected (e.g. some applications of the TTE approach suppose that the time between successive encounters follow a gamma distribution, e.g., Moeller et al., 2018). Other methods are design-based estimators (e.g., CTDS) that do not make any distributional assumption on the data (Howe et al., 2017). Moreover, the different authors emphasise different aspects of monitoring, each with its own specific focus. For instance, some estimators account for imperfect detectability (e.g., CTDS, Howe et al., 2017). Others account for the limited recording time predefined in most commercial camera traps, that impairs the possibility to record precisely the encounters duration (e.g., REST, Nakashima et al., 2017). Others, still, stress the importance of modelling the spatial heterogeneity in density (e.g., TTE, Moeller et al., 2018).

Rather than emphasising the differences, I would like to highlight the similarities between the approaches. To do so, I consider a simplified scenario of camera trap monitoring with perfect detectability, in which all traps have the same activation time H. To facilitate their comparison, I reformulate the estimators as simple formulas rather than as the result of more complex estimation procedures such as the maximum likelihood. I also consider the simplistic case where animal movements are generated by the ideal gas model (Hutchinson and Waser, 2007). In this model, each individual is assumed to move at constant speed in a random direction within a two-dimensional space. Under this model, the different estimators are closely related to each other.

The map is presented in Fig. 1. The rest of the paper aims at giving the details that help to understand it.

The REM and REST approaches

Rowcliffe et al. (2008) demonstrated how it is possible to use the ideal gas model to estimate the population density D from a function of the number of encounters Q that occurred during the total activation time A of the traps, the characteristics r, θ of the camera traps (resp. length and angle of their field of view), and the mean travel speed v of animals:

$$\hat{D} = \frac{Q \times \pi}{A \times v \times r(2+\theta)}$$

In the appendix, I show that under the ideal gas model, it is also possible to calculate the mean duration $E(T)$ of an encounter (staying time) from the mean travel speed v of animals and the characteristics r, θ of the camera trap (the resulting equation is showed in the pink box under the REM estimator in Fig. 1). By expressing the density as a function of $E(T)$ instead of v and simplifying, the density can simply be expressed as:

$$D = E(Y) \cdot E(T)/(sH)$$

where $E(Y)$ is the mean number of encounters per trap, s is the area of the trap field of view, and H is the duration of the study period (i.e., the activation time per trap). The REST estimator developed by Nakashima et al. (2017) is based on this equation: it uses the data collected on the

encounters by the traps to estimate $E(Y)$ and $E(T)$ and derive a density estimate, avoiding the need to estimate v. Note that the original REST model is actually more complex as it accounts for the possibility of right-censored staying time (addressing the limitations of commercial video traps, which stop filming after a predetermined time).

The TTE approach and its relationship with the REM approach

Moeller et al. (2018) developed the TTE approach by reshaping the data collected by the camera traps. They divide the study period into sampling occasions, each sampling occasion being itself divided into consecutive sampling periods. To account for the movement rate of animals, each sampling period is set equal to the average length of time $E(T)$ it takes for an animal to cross through the camera's field of view (which is therefore supposed known). They show that, for each sampling occasion, the number of sampling periods until the first encounter can be used to estimate the population density. Although their modelling approach accounts for numerous factors such as the heterogeneity of the density or imperfect detection, I will consider a simplified approach here with perfect detectability and homogenous density (ideal gas model), as before.

Under the ideal gas model, it can be shown that the total number of encounters Q occurring during the study period follows a Poisson distribution of mean $\lambda \cdot A$ (Fig. 1), where A is as before the total activation time of the traps (summed over all traps). Thus, the mean number Q/A of encounters occurring per unit of time is an estimator of λ.

As Moeller et al. (2018), let us discretize the study period in sampling occasions (e.g. lasting one week). However, instead of discretizing each occasion in sampling periods of length $E(T)$, we transform the time variable to $t' = t/E(T)$, maintaining its continuous nature. This transformation ensures that, on average, an encounter lasts exactly one unit of transformed time. Under the ideal gas model, I show in the appendix that there is a simple relationship between the trap characteristics and the mean paths length $\bar{\ell}$ traversed by an animal during an encounter (the resulting formula is given in the pink box between the REM and the TTE estimators in Fig. 1). By definition, the parameter $\bar{\ell}$ corresponds to the distance travelled by the animal during one unit of transformed time: this is the definition of the mean travel speed of the animals. Therefore, replacing v with $\bar{\ell}$ as well as Q/A by $\hat{\lambda}$ in the REM estimator and simplifying, the REM estimator simply becomes the TTE estimator:

$$\hat{D} = \hat{\lambda}/s$$

The core of the TTE approach involves the estimation of λ. As noted above, under the ideal gas model, encounter times are generated by a Poisson process. Consequently, the time between encounters (inter-arrival time) – or equivalently, the time between the beginning of the sampling occasion and the first encounter – follows an exponential distribution with parameter λ (Ross, 1996, p. 64). The TTE approach estimates λ by fitting an exponential distribution to times to the first encounter during each sampling occasion. The modelling approach of Moeller et al. (2018) actually accounts for the possibility of censored values for each occasion (i.e., the fact that there may be no encounters at all with any trap during a given occasion). We then substitute $\hat{\lambda}$ into the TTE estimator.

The CTDS, IS, and AM approaches

The IS approach estimates the density using the number of animal-trap associations rather than the number of encounters (Moeller et al., 2018). The study period of length H is discretized into J instantaneous capture occasions, separated by a time lag of length δ. At each occasion j, the number n_{ij} of animals present in the field of view of the camera trap i is recorded. The density of associations detected by trap i at time j can be estimated with n_{ij}/s_i, where s_i is the surface area of its field of view. An estimator of the population density is obtained by averaging the density of associations across all M traps and J occasions:

$$\hat{D} = \frac{1}{J \cdot M} \sum_{i=1}^{M} \sum_{j=1}^{J} \frac{n_{ij}}{s_i} = \frac{1}{J \cdot M} \sum_{i=1}^{M} \frac{n_i}{s_i} \tag{1}$$

where $n_i = \sum_{j=1}^{J} n_{ij}$.

Note that the AM approach of Campos-Candela et al. (2018), which estimates the density by averaging the number of animals counted per frame, is basically identical to the IS approach. The AM approach is actually a more complex modelling approach, accounting for environmental variations between cameras, but our assumption of the ideal gas model eliminates such variations, making the AM approach identical to the IS approach (see also equation (4) in Santini et al., 2022). We therefore refer to these two approaches as the IS/AM estimator.

The CTDS approach is also similar to these estimators. Howe et al. (2017) showed how the distance sampling methodology, which accounts for imperfect detectability of animals, can be used in the context of camera trap monitoring. These authors proposed to fit a detection function to a dataset of sampled distances between detections and each trap, giving the probability of detection of an animal as a function of its distance to the trap. An overall probability of detection $\hat{P}_i$ for the whole field of view can be estimated from this detection function. Then, the classic distance sampling estimator can be used:

$$\hat{D} = \frac{2\delta \sum_{i=1}^{M} n_i}{\theta r^2 \sum_{i=1}^{M} H \hat{P}_i}$$

To get a better understanding of the relationship of this estimator with other estimators, we modify it slightly. Note that $s = r^2\theta/2$ is the surface area of the field of view of the camera trap. Moreover, the effective surface s_i of the trap i can be estimated with $s \cdot \hat{P}_i$, so that the CTDS estimator becomes:

$$\hat{D} = \frac{1}{J} \frac{\sum_{i=1}^{M} n_i}{\sum_{i=1}^{M} s_i} \tag{2}$$

Comparing this equation with equation 1, we can see that the CTDS and IS/AM estimators are not identical. The CTDS estimator is equal to the ratio of the number of associations summed over all traps for each occasion divided by the sum over all traps of the efficient surface of the traps. It is a ratio estimator (Thompson, 2002, p. 68). On the other hand, the IS/AM estimator is the mean across all traps of the ratios of the number of associations per trap divided by the surface of the trap. It is a mean-of-the-ratios estimator (Thompson, 2002, p. 84). In design-based estimation, it is well-known that these two estimators are biased, but that the ratio estimator is in general less biased than the mean-of-ratios estimator (Cochran, 1977) and less sensitive to small areas (Fewster et al., 2009). However, the complex relationship between density and detectability (e.g. animals may occur more frequently in places where they are less detectable)

in many studies may render things more complicated, especially in model-based contexts. Thus, simulations may be required to decide which estimator is the most suitable in practice. Anyway, in our case, as we suppose perfect detectability of animals, $s_i = s$ and these two estimators become identical.

Relationship of IS/AM/CTDS approaches with the REST approach

We now demonstrate the equivalence of the REST estimator and these CTDS/IM/AS estimators under certain conditions. As before, we assume that all trap fields of view have equal surface areas. This simplifies the three estimators to a function of the total number of associations detected during the study:

$$\hat{D} = \frac{1}{J \cdot M} \frac{\sum_{i=1}^{M} n_i}{s}$$

The main challenge in demonstrating the equivalence between the REST and CTDS/IS/AM estimators arises from the difference in the data that they require: the REST estimator considers encounters, which have a duration, while the CTDS/IS/AM estimator focuses on instantaneous associations. To address this challenge, we assume that the time lag δ separating two successive occasions is very small (e.g., typically of a few seconds in CTDS studies, see Howe et al., 2017). This allows us to approximate each association as a short period of length δ during which an animal is present in the field of view of the camera. Under this assumption, the total duration of presence of animals within the field of view of all camera traps can be estimated by $\widehat{d} = \sum_i n_i \cdot \delta$.

Now, consider the design used for the REST approach, relying on animal-trap encounters. The mean time spent by animals in the field of view of a random camera trap is $E(Y) \cdot E(T)$. Therefore, the total duration of presence of animals within the field of view of all M traps is equal to $d = M \cdot E(Y) \cdot E(T)$. Thus, we can substitute $\sum_i n_i \cdot \delta / M$ for $E(Y) \cdot E(T)$ in the REST estimator, simplify, and arrive at the CTDS estimator. This shows their equivalence (Fig. 1).

The fact that we can estimate $M \cdot E(Y) \cdot E(T)$ by $\sum_i n_i \cdot \delta$ clarifies why encounter-based methods require knowledge of the mean travel speed, while association-based methods do not. Faster moving animals results in more frequent but shorter encounters, yet the total time spent in front of the traps remains constant.

The STE approach and its relationship with the IS/AM approach

As IS/AM and CTDS approaches, the STE approach defines instantaneous sampling occasions separated by a given time-lag, say, δ. Under the ideal gas model, the distribution of animals on the 2D plane can be described by a Poisson point process. By sampling at any time an area s_i, the resulting number of associations in this area follows a Poisson distribution $n_{ij} \sim \mathcal{P}(\mu_i)$, with $\mu_i = D \cdot s_i$. The total number of associations n_i with trap i (summed over all J occasions) is therefore Poisson-distributed $n_i \sim \mathcal{P}(D \cdot J \cdot s_i)$.

It is well-known that the squared distance between points (squared inter-event distance) generated by a Poisson point process follows an exponential distribution with parameter $\pi \cdot D$ (Diggle, 2013, p. 24). Or, equivalently, the squared distance d between any trap on the study area and the closest animal is exponentially distributed with parameter $\pi \cdot D$. In other words, the largest amount of surface area πd^2 centred on the trap without any animal in it is exponentially distributed with parameter D. This property forms the basis of the STE approach.

Consider a given sampling occasion j. We form a sequence of values n_{ij} in a random order. The probability that the first trap in the sequence with an association (i.e. $n_{ij} > 0$) occurs at the k-th sampled trap is also the probability that the amount of sampled space without animal is equal to $\sum_{i'=1}^{k} s_{(i')}$, where $s_{(i')}$ corresponds to the i'-th trap of the sequence, which is exponentially distributed with mean D.

Moeller et al. (2018) therefore propose generating a random sequence of trap ordering at each occasion, to calculate the increasing amount of surface area sampled along the sequence, and to identify the amount of surface area corresponding to the first trap for which the number of associations is greater than 0. They then fit an exponential distribution to the distribution of the amounts of area sampled at each occasion required before an association is detected. The estimated parameter of this exponential distribution is the estimated density. Again, their modelling approach actually accounts for the possibility of censored values for this area (i.e., the fact that there may be no associations at all with any trap at a given occasion). Regardless, under the ideal gas model and corresponding hypothesis of a Poisson distribution of the animals at any time, the relationship between IS and STE is clear.

Conclusion

When we started working on CT data in our team, we were overwhelmed by the multitude of potential approaches to estimate animal density. Several studies highlighted the disparities between these approaches, emphasising the unique characteristics of each method, in terms of data requirements, detection rates, spatial heterogeneity in density, available side information, etc. (see for example Gilbert et al., 2020; Santini et al., 2022; Wearn et al., 2022). However, we missed a global view of how these approaches are interconnected. Why do some methods require the average travel speed of animals and not others, despite relying on the same camera-trap data? Why does the TTE approach require the knowledge of the time required to cross the field of view of camera traps, but not the very similar STE? What are the relationships between IS and CTDS? Building the map of estimators (Fig. 1) allowed us to gain a better understanding of these relationships.

To allow this study of the relationships between estimators, I simplified some of them. For example, the REST estimator that I presented does not correspond exactly to the one presented by Nakashima et al. (2017). However, the REST estimator on Fig. 1 carries the spirit of the method, and I think that it helps to understand how association-based methods and encounter-based methods are related.

Although I focused on the similarities between methods, the user will, of course, also need to consider their differences when choosing the appropriate approach. This choice depends on their specific goals and requirements. While several studies provide valuable guidance (Gilbert et al., 2020; Nakashima, 2022; Santini et al., 2022; Wearn et al., 2022), the map in Fig. 1 offers a complementary perspective. For example, one common criticism with the association model is that it does not allow to account for imperfect detectability (Santini et al., 2022). However, the map shows here that this approach is, in its principle, very similar to the IS and CTDS, which account for this imperfect detectability. So that if the user is interested in association-based methods accounting for detectability, they can consider IS and/or CTDS. The choice between IS and CTDS depends on whether the user prefers a ratio estimator (CTDS) or a mean-of-ratio estimator (IS), and simulations can be used to assess the bias of each method in a specific context.

The choice of the best method also depends on the elements available to the user (Gilbert et al., 2020; Wearn et al., 2022): whether data on the encounters duration are available or not, whether encounter or association data are collected, whether encounter data can be transformed into association data, etc. Thus, the choice between IS and CTDS also depends on whether distance data are available to fit a detection function (CTDS) or not (IS). Note however that while the CTDS estimator is typically used with detection probabilities estimated from detection functions fitted to distance data, it can be adapted to accommodate detection probabilities derived from other methods (e.g., from field experiments).

Finally, this choice in a given context also has to consider the precision of the different available estimators. This work did not consider the different methods available to estimate the variance of the density estimation (e.g., bootstrap, asymptotic properties of maximum likelihood, design-based estimator). Given the multitude of available variance estimation methods, both the practical aspects of their implementation (e.g., bootstrap is often easy to implement) and their performance must be considered. More generally, regarding precision, simulations of camera-trap monitoring of a population with simulated animal movements can help to assess the relevance of camera-trap monitoring and to determine the most suitable density estimator under specific conditions (Nakashima, 2022; Santini et al., 2022).

Note that the map in Fig. 1 is not exhaustive. Other approaches have been developed to estimate density, like the unmarked spatial capture recapture of Chandler and Royle (2013), which uses the spatial correlation between neighbouring traps to identify the activity centers of the home range of non-identifiable animals, and thereby derive a density estimate (although notoriously imprecise, see Gilbert et al., 2020; Wearn et al., 2022). I focused here on methods relying on the number of associations/encounters to estimate the density, because they are among the most widely used in the literature (e.g., Nakashima, 2022; Santini et al., 2022).

In summary, I do not believe that this map identifies which is the best estimator, as I do think that there is no one-size-fits-all solution. However, it provides a framework for understanding how the different methods are related to each other. By understanding the theoretical relationships between different methods, biometricians can develop new hybrid approaches that combine the strengths of multiple methods. Moreover, it will allow users to make more informed decisions when selecting the most appropriate estimator for their specific context.

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Conflict of interest disclosure

The author declare that he complies with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Data, script, code, and supplementary information availability

Supplementary information is available online, on the same bioRxiv page as the preprint (https://doi.org/10.1101/2025.02.28.640755).

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