



Balancing effort and precision

Camera-trap distance sampling performs as well as the random encounter model to estimate population density of ungulates

Jesse Robert Valtteri Pattison

Master's thesis • 60 credits

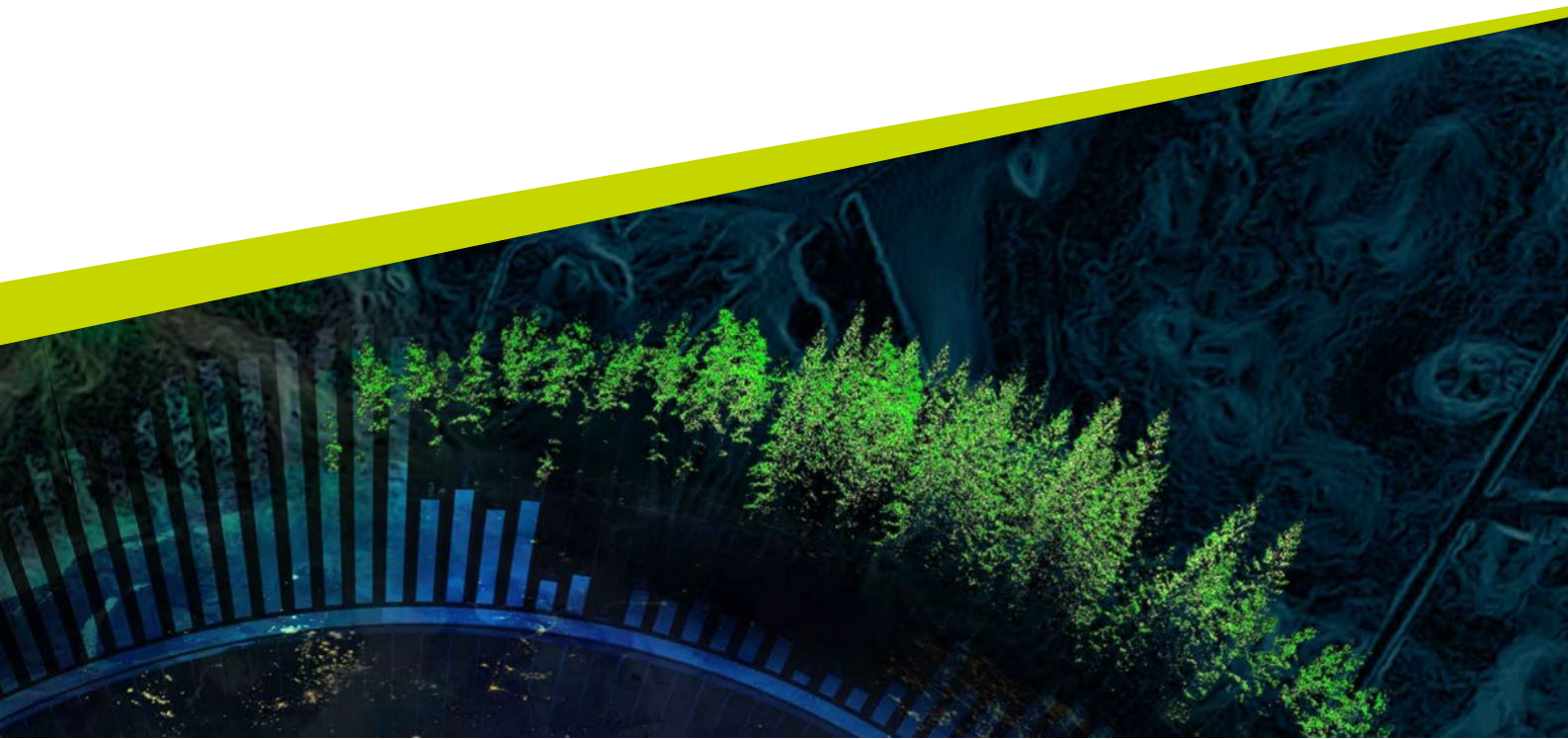
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Abstract

Reliable population densities are vital for effective wildlife management and conservation strategies. In this context, camera traps have become a popular tool for wildlife managers and researchers. The Random Encounter Model (REM) and Camera-Trap Distance Sampling (CTDS) are two methods to estimate the population density of unmarked individuals (i.e., non-individually recognizable). However, these methods have not been previously evaluated together in low-density contexts, such as Scandinavia. Here, I assessed consistency and precision between the two models in six reference areas with five ungulate species in Sweden. I incorporated reported hunting statistics and local knowledge to determine the accuracy of the population density estimates. Further, I assessed the potential impact of extended sampling periods on the models where changes in animal activity are likely to occur due to behavioural and environmental shifts. Comparing REM and CTDS, I did not find significant differences in terms of density estimates in thirteen of sixteen populations. The REM was consistently more precise, with an average coefficient of variation of 0.29 compared to 0.43 for CTDS. Both models aligned with the independent proxies of density. Any potential impact of changes in behaviour influencing density estimates was masked by low model precision for both the REM and CTDS. Given that CTDS requires less effort for image processing, it is an attractive alternative to the REM, especially if the issue of low precision is addressed.

Keywords: wildlife management, population density, remote sensing, behavioural responses, monitoring, camera-trapping

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Abbreviations

AIC	Akaike information criterion
CTDS	Camera-Trap Distance Sampling
CV	Coefficient of variation
DS	Distance Sampling
GLM	Generalized linear model
REM	Random Encounter Model
SAHWM	Swedish Association for Hunting and Wildlife Management
SLU	Swedish University of Agricultural Sciences

1. Introduction

Reliable population density estimates are vital for understanding animal ecology and implementing adaptive wildlife management (Williams et al. 2002; Hofmeester et al. 2017; Santini et al. 2022). Decision makers require accurate estimates of wildlife population density to make informed choices regarding: 1) management decisions, such as the distribution of hunting quotas (Nichols et al. 2007; Baur et al. 2021; Gren et al. 2024); 2) the implementation and assessment of conservation strategies (Nichols & Williams 2006; Reynolds et al. 2011); and 3) navigating risks that are associated with human-wildlife interactions (Nyhus 2016; Pandit et al. 2018). However, it is widely acknowledged that deriving accurate and precise estimates of wildlife populations using traditional methods, such as transect surveys, aerial surveys, and capture-mark-recapture, is time-consuming, expensive, and highly invasive (Caughley 1977; Williams et al. 2002; Palencia et al. 2021). Given these challenges, camera traps have emerged as a valuable tool in wildlife management and conservation in recent decades (O’Connell et al. 2011; Burton et al. 2015). Camera traps have grown in popularity due to their relatively low cost (excluding initial investment) (Palencia et al. 2021), low level of invasiveness (Meek et al. 2016; Caravaggi et al. 2020), ability to continuously record multiple species (Caravaggi et al. 2017), and low effort-to-data volume ratio (Glover-Kapfer et al. 2019), making them an attractive option for wildlife managers and researchers. The utilization of camera traps to estimate density was historically limited to species that were individually distinguishable (e.g., pelage patterns or scars), enabling the application of capture-mark-recapture models to produce density estimates (Karanth 1995). Given that relatively few species are individually recognizable (Rowcliffe et al. 2008), most applications of camera traps focus on questions of relative abundance, behaviour, occupancy or species richness (Gilbert et al. 2021). However, in recent years, significant effort has been devoted to the development of methods to estimate the densities of non-individually recognizable species from camera-trap data (Gilbert et al. 2021; Santini et al. 2022).

Two popular methods for estimating the density of unmarked species are the random encounter model (REM) and camera-trap distance sampling (CTDS) (Rowcliffe et al. 2008; Howe et al. 2017). Both the REM and CTDS estimate density from the frequency with which animals are captured (i.e., encounter rate) while correcting for movement parameters (REM) or detection probability (CTDS) (Palencia et al. 2021). The REM is based on the ideal gas model, envisioning animals as ideal gas particles moving across the landscape, ‘bumping’ into camera traps based on their densities, movement characteristics, and size (Rowcliffe et al. 2008; Gilbert et al. 2021). Since its conception, the REM has become a popular method for deriving density estimates from camera-trap data

(e.g., for red fox, roe deer and wild boar at the European scale, ENETWILD-consortium et al. 2024). CTDS emerged as an extension of distance sampling (DS), which is considered one of the most well-developed and applied methods for estimating animal densities and wildlife monitoring (Buckland et al. 2015; Howe et al. 2017; Palencia et al. 2021). Both traditional DS and CTDS derive density by estimating detection probability and then correcting the observed counts for undetected individuals (Buckland et al. 2015; Howe et al. 2017). Further, CTDS benefits from the existing theoretical framework and statistical software established from DS (Palencia et al. 2021). Although the REM and CTDS both estimate animal density, key differences exist in the parameters they use, thereby influencing their applicability.

Both the REM and CTDS require the estimation of several parameters; however, the explicit quantification of day range (i.e., distance travelled by an animal during a day) is by far the most difficult (Palencia et al. 2021). Initial applications of the REM relied on telemetry data, which underestimates the distance travelled by animals (Rowcliffe et al. 2012). Eventually, methods for estimating day range directly from image data were described, considerably broadening its applicability (Rowcliffe et al. 2016). Estimating day range from image data requires annotating the animal's angle and distance from the camera, significantly increasing data processing costs (Palencia et al. 2021). Conversely, CTDS requires only annotating the distance that the animals are from the camera, thereby reducing time investment during image processing (Palencia et al. 2021). It has been suggested that CTDS may underestimate the density of highly abundant species (Corlatti et al. 2020) but may be more appropriate for low-density species, as it accumulates detections more quickly than the REM (Mason et al. 2022; Palencia et al. 2022). Given the challenges with estimating the parameters required by the REM, it would be beneficial for wildlife managers to know if CTDS could provide similar density estimates and precision in order to maximize limited resources.

Previous research has demonstrated that at high densities, the REM and CTDS models can produce similar density estimates (Palencia et al. 2021; Twining et al. 2022; Miles et al. 2024; Wiegiers et al. 2025), with Palencia and Wiegiers specifically testing these models on ungulate populations of at least 80 individuals per 1000 hectares. However, little is known about their performance at low ungulate densities. Ungulate densities tend to decrease with latitude (Lavsund et al. 2003), making it crucial to evaluate model performance in northern contexts. Low population densities also lead to fewer observations, requiring extended sampling periods to obtain sufficient data for REM and CTDS analyses. Extended sampling periods may violate some model assumptions, especially if ungulate behaviour changes over time. Consequently, assessing how these models perform under extended sampling periods is necessary to ensure reliable density estimates

in low-density contexts. If, compared to the REM, CTDS produces similar results with substantially less effort, it would be preferred as it could provide robust estimates at a lower cost.

In this study, I applied both density estimation methods to five ungulate species (fallow deer *Dama dama*, moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*) across six reference areas in Sweden. The camera traps were part of a national monitoring program managed by the Swedish Association for Hunting and Wildlife Management (SAHWM). Of particular interest is that this project marks the first application of CTDS to ungulates in Sweden. I compared the REM and CTDS in terms of both their density estimates and relative precision. I made the following hypotheses:

- (1) The REM and CTDS will produce similar results both in terms of the density estimate and model precision.
- (2) Density estimates from REM and CTDS will be similar to independently derived density proxies.
- (3) Ungulate density will decrease with increasing latitude.

Additionally, through a series of case studies, I explored the impact of long sampling periods during which ungulate behaviour is likely to shift and potentially bias key parameter estimates. Here, I hypothesized that:

- (4) The presence of snowfall will reduce day range estimates, thereby inflating REM density estimates. The CTDS density estimate will be less influenced, as it does not directly incorporate movement patterns into its density estimation.
- (5) During the rut period, the day range will increase, which will reduce the REM density estimate compared to periods of regular activity. The CTDS density estimate will be less influenced, as it does not directly incorporate movement patterns into its density estimation.

2. Methods

2.1 Camera-trap surveys

In this study, I analysed data from six reference areas across Sweden. The reference areas were located in the counties of Gävleborg, Jämtland, Norrbotten, Östergötland, Skåne and Värmland (Figure 1). All camera traps (Orion 4G, Hunter, Stockholm, Sweden) were installed and maintained by personnel from the SAHWM, as part of the national digital wildlife monitoring initiative. Each reference area had between 32 and 36 camera traps, which were deployed from July 2023 to December 2023 (Appendix 1). The camera trap placement was determined using a systematic sampling design, in which the camera traps were deployed in a grid approximately two kilometres apart and randomly placed with respect to animal movement. The cameras were attached to a pole or tree approximately 80 cm off the ground, and their sensitivity was set to medium. The cameras were set to operate continuously throughout the day and take five consecutive images when triggered.

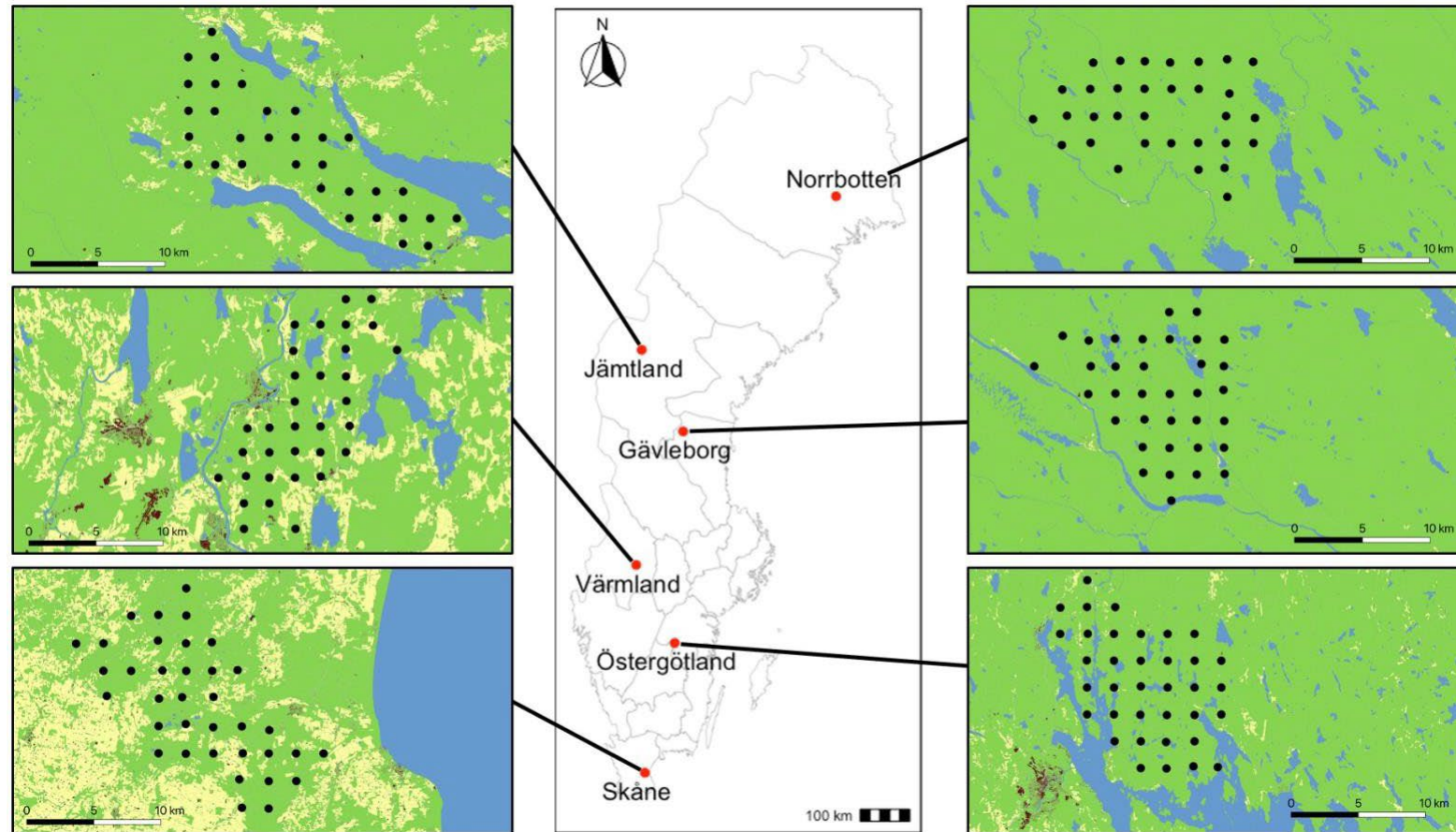


Figure 1: Map of reference areas and camera-trap locations. The centre map depicts the location of the six reference areas in Sweden. The side panels show each reference area with camera-trap locations represented as black dots, green represents forest cover, blue represents water bodies, light yellow represents arable land and brown represents urban development.

2.2 Camera-trapping and data processing

All images were initially processed by the Megadetector algorithm to identify those that contained animals (Beery et al. 2019). Trapper AI then processed the images containing animals to the species level (Bubnicki et al. 2016). Finally, these species identifications were manually checked (and corrected where needed), and information on age class, sex, and behaviour was added by me and personnel at the SAHWM.

During the placement of the cameras, reference images of each camera-trap location were captured. These reference images consisted of the camera-trap's field of view with marking poles in two-meter intervals from the camera to eighteen meters away, following the approach described by Hofmeester et al. (2017). By comparing the images with animals to the reference images, it was possible to estimate the distance the animal was from the camera in two-meter distance intervals. Images where the animal was further than eighteen meters away from the camera were excluded from the analysis. The angular position of the animals in each image was estimated from the centre of the image frame. Once the distance and angle information had been annotated, the data were exported for analysis in R. I, along with personnel at SLU, did these distance and angle estimations. All calculations and analyses were done in R version 4.4.1 (R Core Team, 2024). Images were grouped into the same sequence if they were taken less than five minutes apart; if more than five minutes passed between images, they were grouped into a subsequent sequence. It is recommended that 100 sequences be tracked to derive reasonable precision, with a minimum threshold of 40 sequences to run the analysis (Palencia & Barroso 2024). Fourteen species-reference area combinations fell below the minimum threshold and were excluded from analysis. The final analysis included sixteen combinations: fourteen exceeded the recommended 100 sequences, while the remaining two (roe deer and moose in Gävleborg) had more than 40 sequences.

Due to the large quantity of images captured in Skåne, only images from the end of July to August 31st, 2023, were annotated for all species to reach the 100 sequences minimum. Similarly, for Östergötland, images of roe deer were only annotated from the end of July to August 31st, 2024. All other images of ungulates captured in Östergötland were annotated until December 31st, 2023. This ensured that the recommended number of sequences was reached for all species but reduced the time investment required to annotate the images.

Once both models had generated density estimates for each species-reference area combination, I assessed whether they produced similar density values and precision. The models were considered to produce consistent density estimates if the mean point density fell within the 95% confidence interval of the reciprocal model (Palencia et al. 2021; Twining et al. 2022). To assess model precision, I

calculated the coefficient of variation (CV) for both the REM and CTDS for each species-reference area combination. I then performed a paired t-test to determine whether there was a statistical difference in precision between the two models (Palencia et al. 2021).

2.3 Random Encounter Model parameterization

The REM is based on the ideal gas model, which postulates that the frequency at which gas molecules collide can be predicted given their abundance, their size and their speed (Hutchinson & Waser 2007; Rowcliffe et al. 2008). Put simply, as the abundance, size and speed of gas molecules increase, so does the frequency of collisions. The REM is an extension of this framework, treating animals as ideal gas particles moving across the landscape and randomly encountering camera traps (Rowcliffe et al. 2008; Gilbert et al. 2021). This allows for the REM to estimate density from trapping rate by correcting for variation in animal movement patterns and in the effective detection zone (Rowcliffe et al. 2008, 2011; Hofmeester et al. 2017). The REM is particularly sensitive to error in estimates of day range (Henrich et al. 2022; Morrison et al. 2022; Murphy et al. 2024). A day range estimate that is too high will underestimate density and vice-versa for a day range estimate that is too low (Palencia et al. 2022).

The REM as a function can be expressed as:

$$\hat{D} = \left(\frac{y}{t}\right) * \frac{\pi}{v * r * (2 + \alpha)}$$

In which y is the total number of individuals captured, t is the total survey effort in days, v is the day range in kilometres, r is the effective detection distance in kilometres, and α is the effective detection angle in radians. I estimated all the parameters used in the REM directly from the image data. Following Palencia et al. (2021), I considered each instance of a target species entering the detection zone of a camera-trap as an independent encounter.

Here, I defined day range as the cumulative movement of an animal over a 24-hour period (Klarevas-Irby et al. 2021). I estimated ungulate day range as the product of their mean speed and the proportion of the day they were active (Rowcliffe et al. 2016). The speed of individual ungulates was calculated by summing the distance the animal moved during its capture sequence and then dividing it by the duration of the sequence. Activity pattern curves were created to estimate the proportion of the day that each ungulate species was active (Rowcliffe et al. 2014). Due to Sweden's northern latitude and relatively long survey periods, day length changed throughout the sampling period. To reduce bias introduced by variation in day length, the timestamp data were anchored

using the *solartime* function in the activity package (Vazquez et al. 2019; Rowcliffe 2023). Effective detection distance and angle were estimated from the animal's location in the first image of each sequence (Delisle et al. 2023). The binned distance data were then fitted to a half-normal detection function with a cosine adjustment term of 0, 1 or 2 to calculate effective detection distance (Rowcliffe et al. 2011). The angle data were fitted to either a uniform or half-normal function to calculate the effective detection angle (Rowcliffe et al. 2011).

Once I estimated all the parameters, a REM density estimate was calculated. The 95% confidence intervals for each density estimate were calculated by bootstrapping encounter rate, day range, effective detection distance and effective detection angle with 500 iterations each. Finally, the 2.5th and 97.5th percentiles of the bootstrapped density estimates were calculated to derive the 95% confidence intervals.

2.4 Camera-Trap Distance Sampling parameterization

CTDS is an extension of traditional DS in which stationary camera traps replace human observers to detect moving animals (Howe et al. 2017; Gilbert et al. 2021). As with traditional DS, CTDS utilizes a detection function derived from the distances that detected animals were away from observers during surveying (Buckland et al. 2015). By employing a detection function, an estimate of undetected animals can then be derived, allowing for a density estimate to be calculated (Buckland et al. 2015; Gilbert et al. 2021).

CTDS requires an estimate of the proportion of the day that animals were active and thereby available to be captured by the camera traps (Howe et al. 2017). This can be directly estimated by using the time of day that the animals were captured (Howe et al. 2017). CTDS as a function can be expressed as:

$$\hat{D} = \left(\frac{n}{m}\right) * \left(\frac{2 * d}{w^2 * \theta * p}\right)$$

In which n is the total number of images captured of the target species, m is the sampling effort as defined by the total number of snapshot moments, d is the delay between consecutive images (in this case, a fixed value of two seconds), w is the truncation distance (in this case eighteen meters), θ is the angle of the field of view (in this case 58°) and p is the estimated probability that an animal within the detection zone is detected. In cases where exploratory analysis revealed a lack of observations between zero and two meters, I left-truncated the data at two meters (Howe et al. 2017). The detection probability was calculated by fitting the binned distance data to a half-normal key function (Howe et al. 2017). Specifically, half-normal key functions with 0, 1 and 2 cosine adjustments were

considered; I selected the model in which the detection function was monotonically decreasing with the lowest AIC value (Howe et al. 2017). The CTDS density estimate, along with the 95% confidence intervals, was calculated following the vignette published by Howe et al (2023).

2.5 Evaluation of REM and CTDS with reported hunting statistics

In situations where the actual population size is unknown, it can be challenging to compare between methods (Corlatti et al. 2020). Both the REM and CTDS have been shown to be reliable methods when compared to independent density estimates (Palencia et al. 2021, 2022). However, in this study, acquiring independent density estimates was outside the scope of this project. Instead, reported hunting statistics were utilized as a proxy. I obtained the reported hunting bag statistics from Viltdata (Swedish Environmental Protection Agency 2025). Only roe deer and moose were assessed, as other species were not available in enough reference areas for statistical analysis. To evaluate the consistency between the density rankings derived from REM, CTDS and the reported hunting statistics, a Kendall's coefficient of concordance was calculated.

2.6 Effects of body mass and latitude on density

I applied generalized linear models (GLM) to investigate the potential relationship between latitude and density estimates. The density estimates were obtained from my previous REM and CTDS analyses, along with the latitudes of the reference areas. Both the REM and CTDS densities were modelled as a function of latitude and species. Species as a covariate was included to account for differences in species distribution across Sweden and was not interpreted further. These models were fit with a negative binomial and Poisson models (Hofmeester et al. 2017) and selected based on AIC and residual plot analysis.

2.7 Case studies

In low-density regions like Scandinavia, long sampling periods are often required to obtain sufficient data to produce reliable density estimates. However, seasonal changes in the environment or animal behaviour are known to influence activity levels and, if unaccounted for, may influence trapping rates, causing bias in both the REM and CTDS density estimates (Hofmeester et al. 2019; Henrich et al. 2022). Here, I conducted three case studies to evaluate the impact of snow and mating season on the density estimates produced by both the REM and CTDS models.

The presence of snow is known to restrict animal movement (Melin et al. 2023). The Norrbotten reference area offered an opportunity to explore the impact of snow on the REM and CTDS density estimates as the camera traps were active from July to December. In the Norrbotten reference area, the first permanent winter snowfall was on October 13th, 2023. Following this observation, the image data was then subset into two time periods: pre-snow and snow. I then applied both the REM and CTDS to estimate density as well as the 95% confidence intervals. Finally, the two estimates were compared with each other and with a combined dataset to assess the effect of having an extended sampling period, including a period with and without snow cover.

Moose and roe deer have been shown to elevate their movement rates during their respective mating seasons (Richard et al. 2008; Leblond et al. 2010; Kämmerle et al. 2017). To test the impact of mating season on the REM and CTDS, I chose the Jämtland reference area as the camera traps were active during both species' mating season and non-mating season. For moose, I subset the image data into two periods: before mating season (August 1st to August 31st) and mating season (September 15th to October 15th) (Malmsten et al. 2014). For roe deer, I subset the image into two periods: mating season (July 13th to August 10th) and post-mating season (September 15th to October 15th). I then applied the REM and CTDS to the subset periods of both moose and roe deer to estimate density as well as the 95% confidence intervals. Finally, a combined dataset encompassing the mating and non-mating period for both roe deer and moose was created to assess the effect of having an extended study period, including both mating and non-mating periods.

2.8 Model assumptions

It is important to clarify some of the underlying assumptions made by the REM and CTDS models (Table 1). Because both models use a corrected encounter rate to estimate density, several underlying assumptions are shared (Palencia et al. 2021). Given that most assumptions are shared, a single study design was suitable. Assumptions such as the random deployment of camera traps with respect to animal movement and the independence of observation events were fulfilled through the study design.

An assumption that may be violated is that the camera traps do not influence animal movement or behaviour (Houa et al. 2022). This violation is not uncommon, as it may occur when animals react to the camera (Meek et al. 2016; Henrich et al. 2020). Common reactions include attraction to the camera (e.g., curiosity) or avoidance (e.g., fleeing the detection zone), which violate the assumption that the camera traps do not influence animal movement or behaviour (Houa et al. 2022). However, in practice, attraction events are recorded far more frequently by the camera traps, as fleeing animals generate fewer images before leaving the detection zone. Animals that are attracted to the camera commonly approach and linger close to it, thereby generating a cluster of detections near the camera. This behaviour tends to negatively bias estimates of effective detection distance (REM) and detection probability (CTDS), resulting in a positive bias in estimated density (Delisle et al. 2023). One potential solution would be to exclude consideration of the hazard rate key function when estimating effective detection distance or detection probability, as it often fits spikes of observations near the camera and consequently overestimates density (Delisle et al. 2023). My exploratory analysis revealed that attraction to the camera by target species might have been an issue in my study, as the hazard rate key function likely overestimated density and was therefore excluded from the analysis of effective detection distance and detection probability.

Both the assumptions of perfect detection at zero distance and population closure are problematic in natural settings. To minimize violations of imperfect detection at zero distance, the SAHWM followed the recommendation of Palencia et al. (2021) to set the cameras at an appropriate height and to activate as soon as possible. If the closure assumption is violated and abundance fluctuates, then the REM and CTDS will provide an average density for the entire sampling period (Palencia et al. 2021). A key implicit assumption related to population closure is that the estimated model parameters remain consistent over the sampling period, which is likely violated during extended sampling periods.

Table 1: Summary of the assumptions made for both REM and CTDS models, adapted from Palencia et al. (2021).

Assumption	REM	CTDS
Camera traps are deployed randomly with respect to animal movement	X	X
Camera traps do not influence animal movement or behaviour	X	X
Closed population	X	X
Measurements are precise	X	X
Animals at zero distance are always detected	X	X
Observations are independent events	X	X
Detection distance is recorded from where the animal initially entered the detection zone	X	X
Snapshot moments are selected independently of animal location		X

3. Results

3.1 REM and CTDS Comparison

Sufficient data for generating density estimates were captured for sixteen species-reference area combinations (Appendices 2, 3 and 4). The density estimates for both models ranged from 3.4 individuals per 1000 ha (the REM estimate for roe deer in Gävleborg) to 231.2 individuals per 1000 ha (the REM estimate for red deer in Skåne). As expected, the REM and CTDS exhibited a high level of agreement in their density estimates (Figure 2). Significant differences between the two methods were detected in only three species-reference area combinations: fallow deer in Skåne, roe deer in Värmland, and wild boar in Värmland. Although the density estimates produced by the two models generally agree, some subtle differences seem to reveal more general patterns (Figure 2). The REM produced higher mean density estimates in all six estimates derived from fallow deer, red deer and wild boar. For roe deer and moose, no clear pattern emerged with both REM and CTDS generating higher density estimates. REM had a higher model precision (average CV = 0.29) compared to CTDS (CV = 0.43; $p < 0.001$).

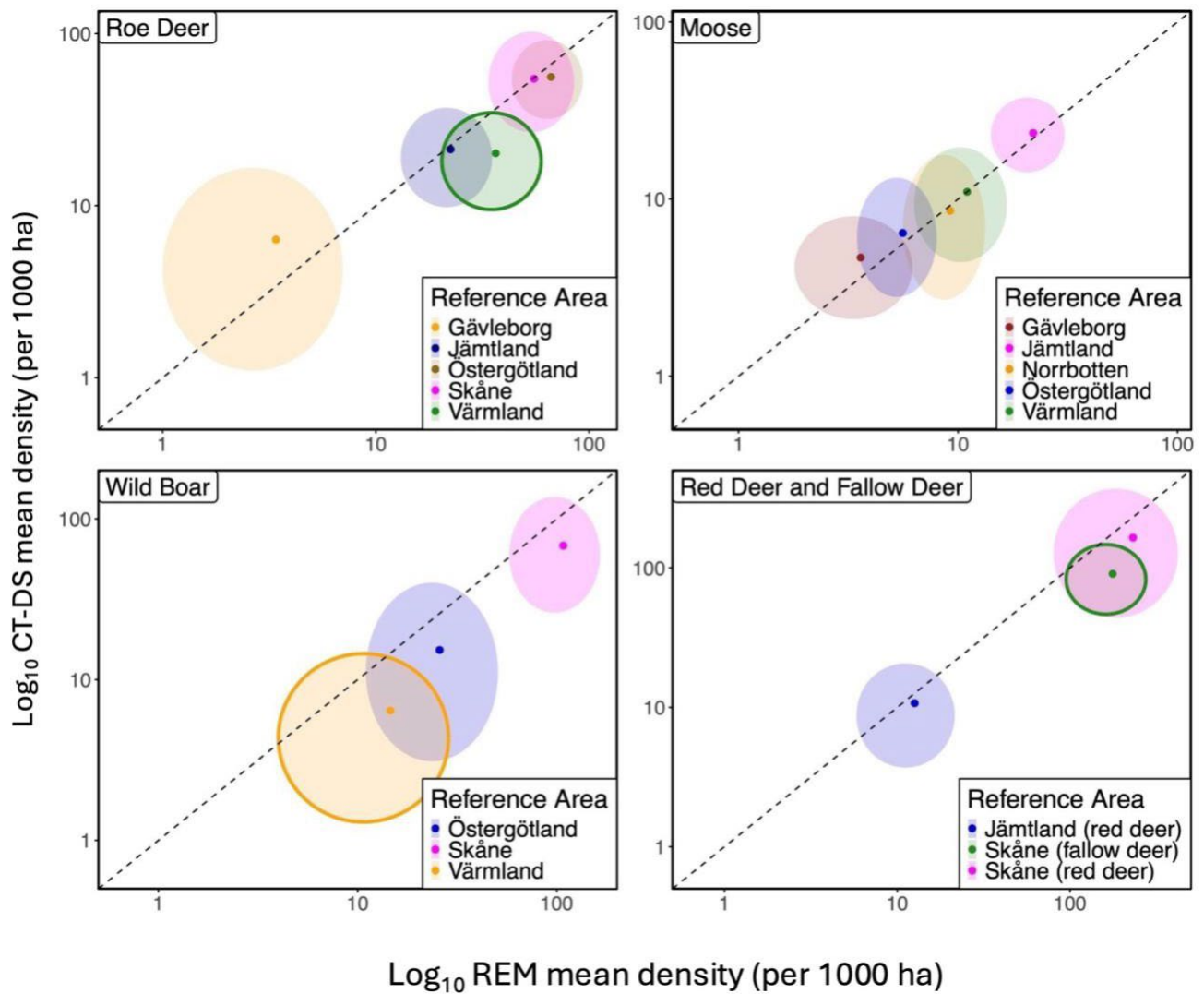


Figure 2: Pairwise comparison of the REM and CTDS density estimates ($\log_{10}$ scale). Dots represent mean density estimates, and translucent ellipses represent 95% confidence intervals. The ellipses with the solid outline indicate species-reference area combinations where the REM and CTDS produced significantly different density estimates. The dashed diagonal line is the line of equality.

3.2 REM and CTDS comparison with reported hunting statistics

The REM, CTDS and reported hunting statistics were ranked for each reference area from highest density to lowest density for both roe deer and moose (Tables 2 and 3). For the roe deer, significant agreement was found in the ranking order between methods (Kendall's coefficient of concordance, $p = 0.03$). For the moose, significant agreement was found in the ranking order between methods (Kendall's coefficient of concordance, $p = 0.03$).

Table 2: Roe deer comparison of REM density estimates, CTDS density estimates and reported harvests by reference area.

Reference area	REM density estimate (ind/1000 ha)	REM rank (highest to lowest)	CTDS density estimate (ind/1000 ha)	CTDS rank (highest to lowest)	Reported hunting yield (harvests/1000 ha)	Reported hunting yield rank
Östergötland	66.3	1	56.0	1	5.2	1
Skåne	55.2	2	54.7	2	4.2	3
Värmland	36.5	3	20.2	4	4.5	2
Jämtland	22.4	4	21.3	3	1.1	4
Gävleborg	3.4	5	6.3	5	0.7	5

Table 3: Moose comparison of REM density estimates, CTDS density estimates and reported harvests by reference area.

Reference area	REM density estimate (ind/1000 ha)	REM rank (highest to lowest)	CTDS density estimate (ind/1000 ha)	CTDS rank (highest to lowest)	Reported hunting yield (harvests/1000 ha)	Reported hunting yield rank
Jämtland	22.0	1	23.6	1	1.9	2
Värmland	11.0	2	11.0	2	1.7	3
Norrbotten	9.2	3	8.6	3	2.2	1
Östergötland	5.6	4	6.4	4	1.4	4
Gävleborg	3.6	5	4.7	5	0.4	5

3.3 Effects of latitude on density

For both models, a negative binomial model was selected based on residual plot analysis and comparison of AIC values. Density decreased with latitude for both the REM (estimate = $-0.26, \pm 0.06$, $p < 0.001$) and CTDS (estimate = $-0.19, \pm 0.06$, $p = 0.002$) estimates (Figure 3).

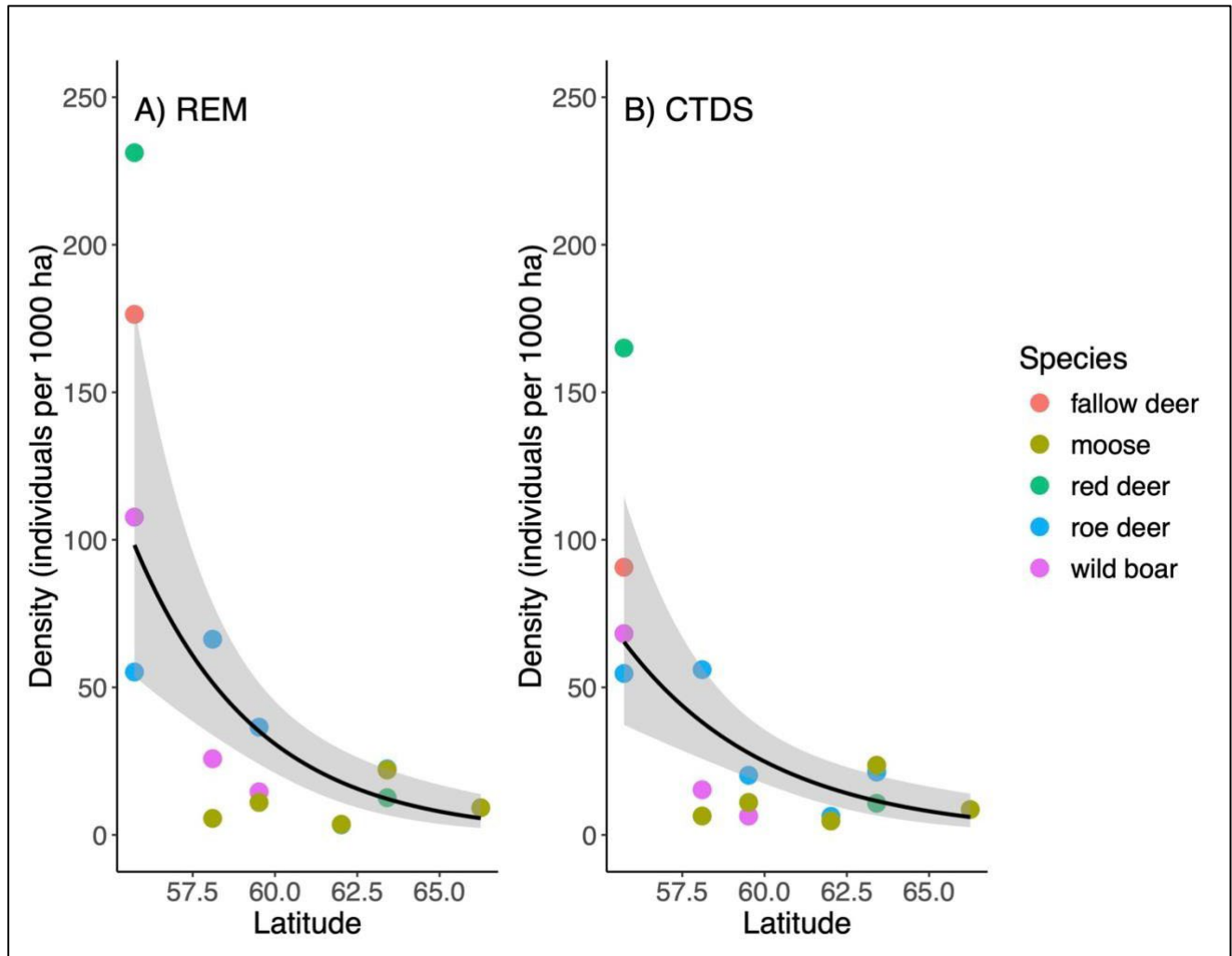


Figure 3: Generalized linear models of the relationship between density and latitude. Panel A (REM) and Panel B (CTDS). The solid points represent mean density values, and translucent ellipses represent 95% confidence intervals. The dashed diagonal line is the line of equality.

3.4 Case Studies

In the three case studies where I explored the potential impact of extended sampling periods, I detected no significant differences in density when applying either the REM or CTDS (Figure 4). Although the individual parameters tended to behave as expected (Appendices 5 and 6), any potential differences were masked by the low precision of the models.

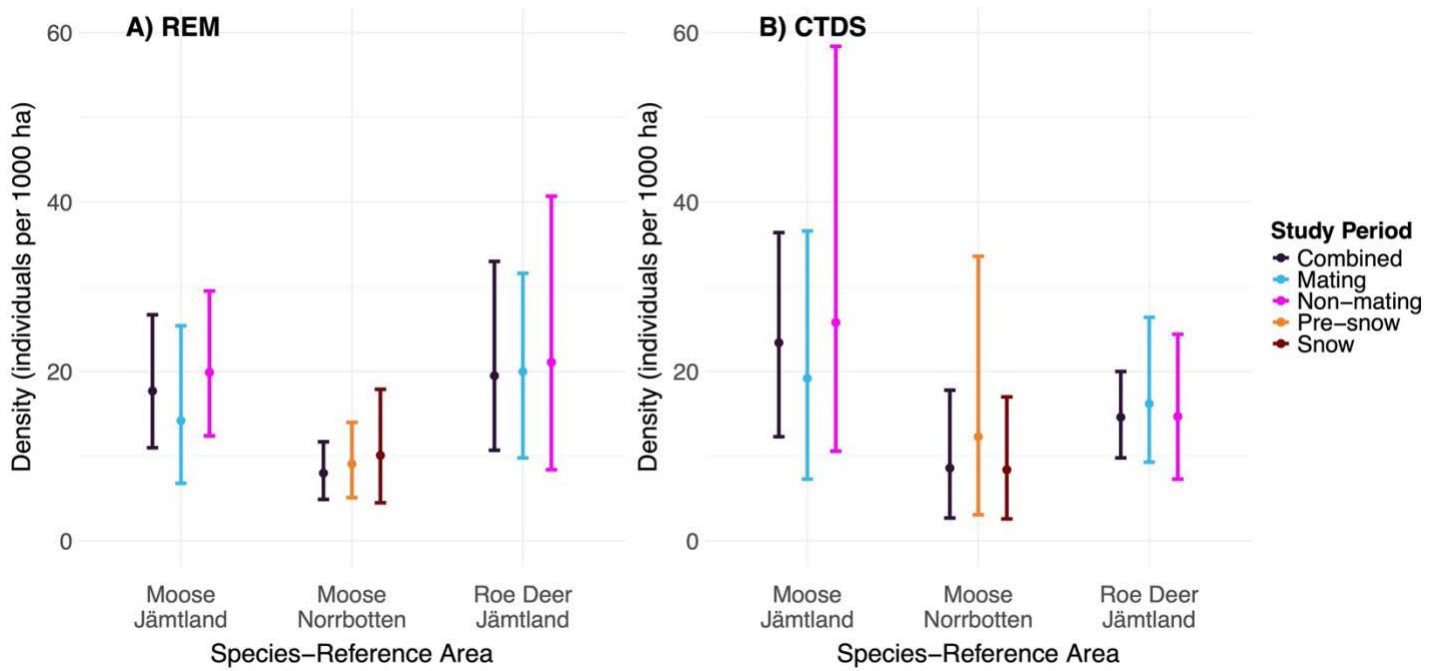


Figure 4: Panel A (REM) and Panel B (CTDS) density estimates from the three case studies. Dots represent mean point density, and the whiskers show the 95% confidence interval.

4. Discussion

The development of methods such as the REM and CTDS has enabled estimation of population density for unmarked species, greatly enhancing the utility of camera traps as a tool for wildlife monitoring (Palencia et al. 2022). However, there is a notable lack of studies that directly compare these methods, especially in areas with low population densities. My work here marks the first direct comparison between the REM and CTDS at low to medium ungulate densities. I compared both methodologies by assessing sixteen species-reference area combinations. I found a high degree of agreement between the two models; however, the REM provided more precise estimates. When compared with reported hunting statistics as independent data and local knowledge, both models displayed a high degree of concordance. Further, density was found to decrease with increasing latitude. Lastly, using three case studies, I explored the impacts of employing extended sampling periods. Although individual model parameters behaved as expected, any potential bias that may have been introduced was masked by low model precision. Finally, if CTDS precision can be improved, it could provide a more cost-effective method compared to the REM.

Since its development, the REM has been widely applied to wild populations (Gilbert et al. 2021; Palencia et al. 2022), whereas CTDS has been applied less frequently (Palencia et al. 2021). My results show a high level of consistency between REM and CTDS in estimated densities, with no significant difference being detected in thirteen of sixteen species-reference area combinations. These results align with previous studies, which also found relative agreement between the two methods (Palencia et al. 2021; Twining et al. 2022; Miles et al. 2024; Wieggers et al. 2025). For example, Palencia and Wieggers found the models performed similarly at high ungulate densities (≥ 80 individuals per 1000 ha). Whereas my density for the species-reference area combinations ranged from 3.4 to 231.2 individuals per 1000 ha, with most estimates below 80 individuals per 1000 ha.

A noticeable trend appeared in all three species-reference area combinations where the models produced significant differences: in all three cases, the REM produced higher density estimates compared to CTDS (Figure 1). This pattern likely indicates that the REM may overestimate densities in these cases. Specifically, in the cases of fallow deer in Skåne and wild boar in Värmland, day range appears to be underestimated (Appendix 3), thereby inflating density estimates (Palencia et al. 2022). For the roe deer in Värmland, the difference does not seem to be driven by an underestimate of day range, but rather a reduced effective detection angle (α), which was estimated to be lower. This reduction in effective detection angle narrows the detection zone and inflates the density estimate (Appendix 3). However, given that most of the effective detection angle

estimates aligned with the manufacturer's specifications, this issue seems to be of secondary importance compared to the estimation of the day range. The day range showed considerable variation and likely contributed to the differences in density between the models, particularly contributing to the REM producing inflated density estimates. Day range is a problematic parameter to estimate for several reasons. First, estimating the day range is both challenging and time-consuming (Gilbert et al. 2021; Palencia et al. 2021). Secondly, day range estimates seem to show a great deal of variation between same-species populations, which REM seems particularly sensitive to (Palencia et al. 2022). Finally, Murphy et al. (2024) found that most published REM density estimates misapplied day range, leading to biased density estimates. Given these challenges, CTDS is an attractive alternative because it does not incorporate day range into its density estimates.

Regarding precision, I found that the REM was more precise than CTDS, which is consistent with previous studies (Palencia et al. 2021; Miles et al. 2024; Wieggers et al. 2025). Specifically, Palencia et al. (2021) reported mean CVs of 0.36 for REM and 0.42 for CTDS, which are similar to my results. This suggests that precision may be consistent in both low and higher density populations. I have no solid interpretation of why REM tends to be more precise than CTDS. It has been recommended that 100 sequences be tracked for both the REM and CTDS to achieve sufficient precision (Bessone et al. 2020; Palencia & Barroso 2024). However, increasing precision may be slightly more nuanced than simply tracking more sequences. For example, despite having well over the recommended number of sequences tracked, red deer in Skåne displayed a relatively low level of precision. This lower level of precision was due to most of the observations being captured by only a few camera traps, indicating a high level of microsite heterogeneity (Hofmeester et al. 2019; Palencia et al. 2021). This is consistent with previous comparisons between the REM and CTDS, where variation in encounter rate between camera traps seemed to be the primary determinant of precision (Palencia et al. 2021; Henrich et al. 2022; Camp et al. 2025). A goal of future studies should be to achieve a CV of 0.20, the recommended threshold for effective wildlife management (Williams et al. 2002; Skalski et al. 2005). Precision can be improved by increasing the number of camera-trap locations, either by deploying more cameras or by rotating camera-trap sites (Schaus et al. 2020; Cappelle et al. 2021; Palencia et al. 2021). To increase the number of observations, the sampling period could be extended, which may improve model precision. However, extending the sampling period may not be ideal as that may introduce more variation into the parameter estimates (e.g., activity patterns, day range), leading to higher uncertainty. Palencia et al. (2021) suggested that the small detection zone of the camera traps causes encounter rates to be particularly sensitive to local microsite conditions. Accounting for local microsite conditions as a covariate could aid in reducing this

source of variation. Despite similarity in the REM and CTDS density estimates, the lack of precision in CTDS requires further consideration.

An interesting pattern emerged regarding the REM and CTDS handling of solitary and gregarious species. Of the species considered in this study, fallow deer, red deer, and wild boar are the most communal, often living in social groups. Notably, two of the three species-reference area combinations that showed a statistical difference between REM and CTDS densities involved these group-living species. Additionally, the REM point densities for these group-living species tended to be higher than the corresponding CTDS point densities. This suggests that social behaviour may be an important factor when assessing which model produced the higher point density estimate. This is broadly consistent with Palencia et al. (2021), who found a similar pattern when estimating ungulate densities in Spain. Further, Chauvenet et al. (2017) demonstrated that REM was particularly sensitive to group size. In contrast, CTDS has shown no such pattern (Bessone et al. 2020). There are several potential reasons why grouping behaviour may disproportionately impact the REM. One possible explanation could be that ungulates that forage in groups tend to spend longer times feeding in quality sites compared to solitary ungulates (Lagory 1986). Therefore, if a group happens to feed within the detection zone of a camera trap, they may spend more time in front of the camera compared to a solitary ungulate. This may impact REM, as a negatively biased day range estimate will inflate density. A potential second explanation is that in a group, each animal has a chance to trigger the camera (Chauvenet et al. 2017). For CTDS, closer individuals may trigger the camera, allowing for the capture of more distant individuals. This could potentially increase detection probability, thereby decreasing the density estimate. A final explanation could be due to different definitions of what constitutes an observation. The REM defines each individual who is captured within the detection zone as an observation (Rowcliffe et al. 2008; Palencia et al. 2022). In comparison, CTDS treats each detection occurring within a photoperiod as an observation (Howe et al. 2017). Although subtle, this distinction may have a greater impact on the REM density estimates, as every individual in the group will be counted, whereas in the CTDS, the effect may be muted, as the observation is not at the individual level. However, it seems that social behaviour can influence density estimates, particularly in the case of REM.

Additionally, my results showed that density decreased with latitude, consistent with previous studies that have demonstrated a decrease in ungulate density with lower productivity and greater winter severity (Lavsund et al. 2003; Hinton et al. 2022). In my study, this pattern is most clearly demonstrated with wild boar. For the other ungulate species assessed, this pattern tended to be evident but not necessarily consistent across all reference areas. As I included species as a categorical covariate in the GLMs, the models accounted for differences in

baseline densities between species. This is because the model sets a separate intercept for each species, while the slope of latitude is shared across all species. By doing this, it is unlikely that the pattern observed is driven by species distribution but rather reflects that, on average across the species, density does indeed decline with latitude. Given that density decreased with latitude, one could expect extended sampling periods to obtain the required number of observations.

The reported hunting statistics were found to have a significant level of concordance with the REM and CTDS in the ranking of reference areas. Previous work has shown that reported hunting statistics can reflect patterns in wild ungulate populations (Rönnegård et al. 2008; Carvalho et al. 2024). Given this context, the high level of concordance in ranking the reference areas indicates modest support for the notion that the REM and CTDS densities broadly reflect actual patterns in ungulate densities. Further, communication with local wildlife managers regarding the REM estimates indicated that the density estimates were generally consistent with their assessments of ungulate density. Notably, the REM estimates for fallow deer and red deer in Skåne, as well as both the REM and CTDS estimates for moose in Jämtland, were thought to be overestimates (F. Ånöstam, personal communication). In these two cases from Skåne, CTDS appeared to perform better. These findings are broadly consistent with previous work, which has demonstrated that both the REM and CTDS can produce reliable density estimates when compared to independently derived estimates (Palencia et al. 2021; Wiegiers et al. 2025). However, it must be mentioned that reported hunting statistics may not be the most appropriate proxy of ungulate density. Hunting in Sweden is not primarily determined by animal density but influenced by cultural norms and co-existence with industries such as agriculture and forestry (Boman & Mattsson 2012). Specifically, for moose, the hunting yields may be more reflective of management goals rather than moose densities (Wikenros et al. 2025). Exploratory analysis of moose observations by hunters, when adjusted for survey effort, showed that the moose observations did not correspond to the reported yield. This indicates that reported hunting yield was more reflective of management goals rather than trends in density. This suggests that reported hunting statistics may not be appropriate as a proxy for density, and perhaps moose observations or the frequency of moose-vehicle collisions may be more suitable. However, these approaches also have limitations, particularly in accessing the appropriate scale for vehicle collisions and the sampling bias introduced by the non-random nature of hunter observations. Given these challenges, future studies should be cautious about utilizing density proxies when attempting to validate their density estimates. Instead, validating density estimates should be done using independently derived density estimates, such as line-transect distance sampling or drive counts (Palencia et al. 2021; Wiegiers et al. 2025). However, direct model validation is rare, as many studies assume the

results are valid based on previous demonstrations of model accuracy (Bessone et al. 2020; Palencia et al. 2021, 2022; Wieggers et al. 2025).

The case studies revealed no detectable difference in the density estimates derived from either REM or CTDS in periods where animal movement patterns were assumed to change. This mirrors findings from Henrich et al. (2022), who suggest that violations of parameter consistency may be masked by low model precision. Despite the potential for parameter inconsistency to occur during an extended sampling period, the subset periods generally reflect the expected seasonal patterns. For example, periods where ungulates are expected to be more active (e.g., pre-snow period and rut-periods) correspond with a higher level of observations. This aligns with a core assumption of the REM, which postulates that the greater an ungulate's day range, the more likely it is to pass through a detection zone (Rowcliffe et al. 2008). Alternatively, CTDS derives an estimate of activity from the proportion of the day that ungulates were active (Howe et al. 2017). During rut periods, both the roe deer and moose in Jämtland seemed to display increased levels of activity, consistent with day range matching studies of other European ungulates (Csányi et al. 2022). The moose in Norrbotten appears to be the exception, with the estimated activity seemingly increasing during the snow period despite the day range apparently shrinking. This phenomenon could be explained by snow limiting the movement range of moose, while at the same time, increased energy expenditure may require a greater need for foraging in the presence of snow, thereby increasing activity level. An additional observation regarding the moose in Norrbotten was that the activity level in the combined data was higher than both the pre-snow and snow periods. This suggests that if animal activity patterns shift during an extended study period, the activity level estimate will be inflated when pooling the data (Vazquez et al. 2019). Further, given the extended sampling periods required in this study, it is likely that the assumption of population closure was violated. This is particularly true given that for several of the species-reference area combinations assessed, the sampling period spanned the hunting season. In such cases, if ungulate density changes during the sampling period, both the REM and CTDS provide an estimate of the average density across the entire sampling period, rather than a density estimate prior to or post-hunting. (Palencia et al. 2021). The three case studies illustrate this averaging effect; for example, the parameter estimates shifted as one might expect, but the density estimates tended to remain similar. This consistency reveals compensatory effects, where seasonal changes in parameter estimates (e.g., day range) are offset by the number of detections, resulting in relatively stable averages of density across the study period.

The cost-effectiveness of any monitoring program is a crucial consideration for wildlife managers who work with limited budgets (Nichols & Williams 2006; Lindenmayer & Likens 2010). The process of annotating the image data is the

most time-consuming when working with camera traps (Steenweg et al. 2017; Palencia et al. 2021). The REM is more time-consuming as it requires that all images be annotated with both distance and angle to estimate the necessary parameters (e.g., day range, effective detection distance, and effective detection angle) (Rowcliffe et al. 2016; Palencia et al. 2019). Conversely, CTDS requires only the distance to be recorded, which significantly reduces the image processing time (Howe et al. 2017; Palencia et al. 2021). Palencia et al. (2021) suggest that, in terms of data analysis, the CTDS requires slightly more effort due to exploratory analysis and model selection. However, I suggest that both models require a similar level of effort regarding exploratory analysis and model selection, especially if effective detection distance is estimated using a detection function as described by Hofmeester et al. (2017). Thus, the reduction in image processing time may make CTDS a preferable method over the REM in the future.

Currently, the primary limitation of CTDS is its tendency to have lower precision than the REM. Future research should investigate the drivers of this pattern and develop additional techniques that improve model precision. If novel techniques manage to increase the precision of CTDS, the model will be an attractive option for wildlife managers in low-density regions. In my study, both the REM and CTDS had a high level of agreement in their density estimates. However, the day range estimates required for the REM seemed to be a culprit when the models diverged, causing inflated REM density estimates. CTDS does not require an estimate of day range, potentially increasing its suitability. When compared with reported hunting statistics, both models performed well, indicating that their estimates reflect actual patterns in ungulate density. When compared with local knowledge, it could be argued that CTDS performed slightly better, as REM was thought to have been slightly more prone to overestimating density in some cases. CTDS has been demonstrated to be more cost-effective than REM, as less effort is required for image annotation. Also, CTDS has explicitly been recommended for low-density species as it can accumulate observations more quickly (Palencia et al. 2021). Taken together, these factors indicate that CTDS presents a promising alternative to REM for wildlife managers in low-density areas, such as Sweden, especially if CTDS precision is improved.

5. Conclusion

In this thesis, I assessed density estimates derived from the REM and CTDS in Sweden, where ungulate densities tend to be low. I found that the REM and CTDS produced similar results in terms of density estimates. However, the REM estimates were more precise compared to CTDS. The models were found in relative concordance with reported hunting statistics and with local wildlife management. Further, my results indicated that density decreased with latitude, which likely contributed to the need for extended sampling periods. For both the REM and CTDS low model precision masked any potential impact of changes in behaviour over extended sampling periods. In terms of cost-effectiveness, the CTDS requires less effort in terms of image annotation, which may constitute a more cost-effective method of deriving density estimates, proving to be an attractive method for wildlife managers. Future research should seek to improve the precision of CTDS, which would enhance its applicability for monitoring wildlife. The continued development and refinement of methods utilizing camera traps to estimate the density of unmarked species is critical for informed wildlife management and conservation.

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Popular science summary

Understanding how many animals live in an area is key to successful wildlife management and conservation. However, it is not easy to estimate how many animals are in a particular area. Camera traps have become a popular tool to aid ecologists in estimating population density. Historically, camera traps could only provide density estimates of individually recognizable animals. However, in recent years, models have been developed that allow for non-individually recognizable animals. I compared two such models, the Random Encounter Model (REM) and Camera-Trap Distance Sampling (CTDS). I used camera-trap data from six reference areas in Sweden to compare their density estimates of fallow deer, moose, red deer, roe deer and wild boar. Further, I compared the results from both models with reported hunting statistics and local experts. I also examined whether long sampling periods, which capture season changes in animal behaviour, affected either model's results. I found that both models produced very similar density estimates. I also found that they matched well with the reported hunting statistics and local knowledge. Further, I found that both models lacked the necessary precision to be impacted by seasonal changes in animal behaviour. The CTDS requires less effort when it comes to data processing, making it an attractive option. This research could help ecologists and wildlife managers produce animal density estimates more cost-effectively, which is crucial for all wildlife management, as they are working with limited budgets.

Appendix 1

Appendix table 1: Summary of camera trap deployments by reference area.

Reference Area	Number of camera traps	Sampling period in 2023	Latitude	Longitude
Gävleborg	35	July - October	62.0° N	15.4° E
Jämtland	32	July - October	63.4° N	14.0° E
Norrbottn	32	July - December	66.3° N	21.6° E
Östergötland	36	July - December	58.1° N	15.1° E
Skåne	36	July - August	55.7° N	14.0° E
Värmland	33	August - December	59.5° N	13.6° E

Appendix 2

Appendix table 2: The REM and CTDS density estimates (mean number of individuals per 1000 ha) of each species by reference area, including the bootstrapped 95% confidence intervals. In bold are the species-reference area combinations where the mean density estimate of one model lies outside of the 95% confidence interval of the other model.

Species	Reference area	REM point density estimates in individuals/1000 ha (95% confidence intervals)	CTDS point density estimates in individuals/1000 ha (95% confidence intervals)
Fallow Deer	Skåne	176.4 (94.9 - 274.3)	90.7 (46.6 - 147.2)
Moose	Gävleborg	3.6 (1.8 - 6.2)	4.7 (2.1 - 8.0)
Moose	Jämtland	22.0 (14.1 - 30.6)	23.6 (14.2 - 37.5)
Moose	Norrbottn	9.2 (5.6 - 13.3)	8.6 (2.7 - 17.8)
Moose	Östergötland	5.6 (3.5 - 8.0)	6.4 (2.8 - 13.2)
Moose	Värmland	11.0 (6.3 - 16.7)	11.0 (4.4 - 19.6)
Red Deer	Jämtland	12.6 (5.8 - 21.5)	10.7 (3.7 - 20.7)
Red Deer	Skåne	231.2 (80.2 - 421.6)	165.0 (43.9 - 370.0)
Roe Deer	Gävleborg	3.4 (1.0 - 7.0)	6.3 (1.1 - 16.6)
Roe Deer	Jämtland	22.4 (13.1 - 35.1)	21.3 (9.8 - 37.1)
Roe Deer	Östergötland	66.3 (43.4 - 93.7)	56.0 (31.9 - 91.7)
Roe Deer	Skåne	55.2 (33.7 - 85.1)	54.7 (26.7 - 102.7)
Roe Deer	Värmland	36.5 (20.4 - 59.6)	20.2 (9.5 - 34.7)
Wild Boar	Östergötland	25.8 (11.0 - 50.7)	15.3 (3.1 - 40.1)
Wild Boar	Skåne	107.7 (57.7 - 164.5)	68.2 (26.1 - 136.9)
Wild Boar	Värmland	14.6 (4.0 - 28.6)	6.4 (1.3 - 14.5)

Appendix 3

Appendix table 3: The REM parameter estimates for each species-reference area combination. In bold are the species-reference area combinations where the mean density estimate of one model lies outside of the 95% confidence interval of the other model.

Species	Reference area	Density per 1000 ha (95% confidence intervals)	y – Number of individuals captured	t – Camera trap days	r – Effective detection distance in meters (95% confidence intervals)	Key function	α – Effective detection angle (radians)	Proportion of the day active	Speed estimate in kilometers per hour	v – Day range (km)
Roe Deer	Skåne	55.2 (33.7 – 85.1)	424	1424	6.2 (5.5 - 7.0)	hn2	1.01	0.54	0.70	9.1 (7.7 - 10.8)
Roe Deer	Östergötland	66.3 (43.4 - 93.7)	517	2502	6.2 (5.7 - 6.5)	hn1	0.93	0.48	0.47	5.5 (4.7 - 6.6)
Roe Deer	Värmland	36.5 (20.4 - 59.6)	587	4435	5.8 (5.4 - 6.1)	hn1	0.79	0.57	0.52	7.1 (6.1 - 8.5)
Roe Deer	Gävleborg	3.4 (1.0 - 7.0)	61	3383	7.1 (6.1 - 8.3)	hn0	1.01	0.64	0.51	7.8 (5.3 - 13.2)
Roe Deer	Jämtland	22.4 (13.1 - 35.1)	362	3075	4.5 (4.1 – 5.0)	hn2	1.01	0.64	0.79	12.2 (9.9 - 15.9)
Fallow Deer	Skåne	176.4 (94.9 - 274.3)	557	1424	5.9 (5.4 – 6.5)	hn1	1.01	0.28	0.58	3.9 (3.4 - 4.8)
Wild Boar	Skåne	107.7 (57.7 - 164.5)	364	1424	5.4 (4.9 – 6.0)	hn1	1.01	0.24	0.81	4.6 (3.7 - 5.7)
Wild Boar	Östergötland	25.8 (11.0 - 50.7)	396	5701	5.1 (4.7 – 5.6)	hn1	0.64	0.42	0.63	6.3 (5.2 - 7.8)

Wild Boar	Värmland	14.6 (4.0 - 28.6)	183	4435	6.4 (5.4 - 8.1)	hn1	1.01	0.25	0.76	4.6 (3.3 - 6.2)
Red Deer	Skåne	231.2 (80.2 - 421.6)	396	1424	5.1 (4.7 - 5.5)	hn1	1.01	0.24	0.44	2.5 (2.0 - 3.1)
Red Deer	Jämtland	12.6 (5.8 - 21.5)	218	3075	6.3 (5.8 - 6.8)	hn0	1.01	0.76	0.51	9.3 (7.1 - 12.4)
Moose	Östergötland	5.6 (3.5 - 8.0)	149	5701	6.4 (5.7 - 7.6)	hn1	1.01	0.64	0.50	7.6 (5.9 - 10.4)
Moose	Värmland	11.0 (6.3 - 16.7)	126	4435	6.2 (5.5 - 7.3)	hn1	1.01	0.50	0.36	4.3 (3.4 - 6.1)
Moose	Gävleborg	3.6 (1.8 - 6.2)	76	3383	7.4 (6.4 - 8.4)	hn0	1.01	0.45	0.82	8.8 (6.4 - 12.2)
Moose	Jämtland	22.0 (14.1 - 30.6)	271	3075	7.4 (6.8 - 8.0)	hn0	1.01	0.42	0.55	5.6 (4.7 - 6.8)
Moose	Norrboten	9.2 (5.6 - 13.3)	125	4413	5.9 (5.3 - 6.9)	hn1	1.01	0.67	0.34	5.5 (4.3 - 7.3)

Appendix 4

Appendix table 4: The CTDS parameter estimates for each species-reference area combination.

Species	Reference area	Density per 1000 ha (95% confidence intervals)	n – Total number of capture images	m – Number of snapshot moments	w – truncation distance (km)	θ – detection angle (radians)	Left truncation of first two meters	Key function	p - Probability of detection
Roe Deer	Skåne	54.7 (26.7 - 102.7)	1321	33305781	0.018	1.01	Yes	hn1	0.09
Roe Deer	Östergötland	56.0 (31.9 - 91.7)	2136	52032835	0.018	1.01	No	hn1	0.09
Roe Deer	Värmland	20.2 (9.5 - 34.7)	1711	109660005	0.018	1.01	Yes	hn1	0.10
Roe Deer	Gävleborg	6.3 (1.1 - 16.6)	296	93858222	0.018	1.01	Yes	hn1	0.06
Roe Deer	Jämtland	21.3 (9.8 - 37.1)	923	85239588	0.018	1.01	Yes	hn2	0.06
Fallow Deer	Skåne	90.7 (46.6 - 147.2)	1695	17464097	0.018	1.01	Yes	hn1	0.13
Wild Boar	Skåne	68.2 (26.1 - 136.9)	671	14497254	0.018	1.01	Yes	hn2	0.08
Wild Boar	Östergötland	15.3 (3.1 - 40.1)	901	104970377	0.018	1.01	Yes	hn1	0.07

Wild Boar	Värmland	6.4 (1.3 - 14.5)	737	48357497	0.018	1.01	Yes	hn0	0.24
Red Deer	Skåne	165.0 (43.9 - 370.0)	1708	14476761	0.018	1.01	No	hn1	0.09
Red Deer	Jämtland	10.7 (3.7 - 20.7)	996	101184389	0.018	1.01	Yes	hn0	0.11
Moose	Östergötland	6.4 (2.8 - 13.2)	1001	160423004	0.018	1.01	No	hn0	0.12
Moose	Värmland	11.0 (4.4 - 19.6)	790	92920587	0.018	1.01	No	hn1	0.09
Moose	Gävleborg	4.7 (2.1 - 8.0)	354	65395334	0.018	1.01	No	hn0	0.14
Moose	Jämtland	23.6 (14.2 - 37.5)	1378	56320728	0.018	1.01	Yes	hn0	0.13
Moose	Norrbottn	8.6 (2.7 - 17.8)	885	123488593	0.018	1.01	No	hn0	0.10

Appendix 5

Appendix table 5: The REM parameter estimates for the case studies.

Species-reference area	Sampling period	Density per 1000 ha (95% confidence intervals)	y – Number of individuals captured	t – Camera trap days	r – Effective detection distance in meters (95% confidence intervals)	Key function	α – Effective detection angle (radians)	Proportion of the day active	Speed estimate in kilometers per hour (95% confidence intervals)	v – Day range in kilometers (95% confidence intervals)
Moose-Norrbotten	pre-snow	9.1 (5.1 - 14.0)	68	2004	7.5 (6.4 - 8.7)	hn0	1.01	0.48	0.45 (0.34 - 0.63)	5.16 (3.9 - 7.2)
Moose-Norrbotten	snow	10.1 (4.5 - 17.9)	57	2408	5.7 (4.7 - 6.7)	hn0	1.01	0.66	0.27 (0.20 - 0.38)	4.27 (3.2 - 6.0)
Moose-Norrbotten	combined	8.0 (4.9 - 11.7)	125	4412	6.7 (5.9 - 7.5)	hn0	1.01	0.67	0.34 (0.27 - 0.46)	5.47 (4.4 - 7.3)
Roe deer-Jämtland	mating season	20.0 (9.8 - 31.6)	108	687	5.6 (5.0 - 6.2)	hn0	1.01	0.61	1.00 (0.73 - 1.48)	14.6 (10.7 - 21.5)
Roe deer-Jämtland	not mating season	21.1 (8.4 - 40.7)	101	961	5.8 (5.1 - 6.5)	hn0	1.01	0.47	0.82 (0.51 - 1.38)	8.9 (5.8 - 15.5)
Roe deer-Jämtland	combined	19.5 (10.7 - 33.0)	209	1648	5.7 (5.3 - 6.1)	hn0	1.01	0.55	0.89 (0.66 - 1.22)	11.9 (8.8 - 16.2)
Moose-Jämtland	not mating season	19.9 (12.4 - 29.5)	79	992	7.6 (6.4 - 8.9)	hn0	1.01	0.44	0.51 (0.41 - 0.67)	5.5 (4.3 - 7.1)
Moose-Jämtland	mating season	14.2 (6.8 - 25.4)	80	961	7.6 (6.4 - 8.8)	hn0	1.01	0.55	0.61 (0.40 - 0.98)	8.0 (5.3 - 13.0)
Moose-Jämtland	combined	17.7 (11.0 - 26.7)	159	1953	7.6 (6.8 - 8.5)	hn0	1.01	0.47	0.56 (0.43 - 0.72)	6.3 (4.9 - 8.2)

Appendix 6

Appendix table 6: The CTDS parameter estimates for the case studies.

Species-reference area	Sampling period	Density per 1000 ha (95% confidence intervals)	n – Total number of capture images	m – Number of snapshot moments	w – truncation distance (km)	θ – detection angle (radians)	Left truncation of first two meters	Key function	p - Probability of detection (95% confidence intervals)
Moose-Norrbottn	pre-snow	12.3 (3.1-33.6)	495	42333703	0.018	1.01	No	hn0	0.12 (0.10-0.13)
Moose-Norrbottn	snow	8.4 (2.6-17.0)	390	67755701	0.018	1.01	No	hn0	0.08 (0.07-0.09)
Moose-Norrbottn	combined	8.6 (2.7-17.8)	885	123488593	0.018	1.01	No	hn0	0.10 (0.09-0.11)
Roe deer-Jämtland	mating season	16.2 (9.3-26.4)	284	17978379	0.018	1.01	No	hn0	0.12 (0.10-0.13)
Roe deer-Jämtland	not mating season	14.7 (7.3-24.4)	320	19444324	0.018	1.01	No	hn0	0.14 (0.12-0.15)
Roe deer-Jämtland	combined	14.6 (3.6-9.8)	604	39439509	0.018	1.01	No	hn0	0.13 (0.12-0.14)
Moose-Jämtland	not mating season	25.8 (10.6-58.4)	484	18996085	0.018	1.01	No	hn0	0.12 (0.10-0.14)
Moose-Jämtland	mating season	19.2 (7.3-36.6)	457	22914980	0.018	1.01	No	hn0	0.13 (0.11-0.14)
Moose-Jämtland	combined	23.4 (12.3-36.4)	941	39801781	0.018	1.01	No	hn0	0.12 (0.11-0.13)

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