Biological Conservation 321 (2026) 111988

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Challenges in estimating wolf population size using spatial count models and camera trap data

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ARTICLE INFO

Keywords:
Wolf conservation
Camera trapping
Spatial count models
Large-scale population monitoring
Abundance estimation
Conservation practice

ABSTRACT

Accurate abundance estimates are essential for wildlife conservation but remain difficult to obtain for wide-ranging and elusive species. Camera-traps (CT) are one of the most popular tools to study wildlife. However, the usefulness of CT data to estimate population sizes for species without individual marks remains debated. Several statistical methods showed promise in simulation studies, but researchers urged caution, and large-scale applicability remains unclear. This work aims to evaluate the use of Bayesian Spatial Count (SC) models to estimate the wolf (*Canis lupus*) population size in the Italian Alps using CT data collected through an opportunistic sampling design. A total of 755 CT were deployed across the entire range of occurrence during 2020/2021. Thanks to the availability of independent abundance estimates during the same period, we were able to investigate the effect of including prior information on the quality of large-scale population size estimates. SC models failed to provide accurate population size estimates, largely overestimating abundance, especially when using non-informative priors. While including informative priors on the effect of density covariates slightly improved estimates, providing informative priors for the spatial scale parameter led to no improvement, contrary to previous suggestions. Our findings highlighted the importance of using an adequate sampling design and accounting for individual heterogeneity in detectability within the population. Overall, SC models based on CT data seem not yet suitable for large-scale monitoring of unmarked, socially structured species like wolves, but improved sampling designs and methodological advances may increase their applicability for cost-effective population assessment.

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https://doi.org/10.1016/j.biocon.2026.111988
Received 21 June 2025; Received in revised form 29 May 2026; Accepted 20 June 2026
Available online 27 June 2026

1. Introduction

Accurately estimating population size is a fundamental goal of wildlife conservation and management (Williams et al., 2002). Abundance estimates are highly sought after as they are needed for effective decision-making (Nichols, 2014), species conservation (Bonebrake et al., 2010) and evaluating the success of conservation efforts (Mace et al., 2008). Traditional approaches to abundance estimation rely on different types of data, including direct counts (Krebs, 1999), live-trapping (Hayne, 1949; Wiewel et al., 2009), and transect surveys (Burnham et al., 1980). These data can be analysed using various statistical approaches, ranging from distance sampling (Buckland et al., 2005) to capture-recapture models (Seber, 1982), which explicitly account for imperfect detection (Schwarz and Seber, 1999). While these approaches have proven to be effective, collecting the necessary data is labour-intensive and costly, particularly over large spatial scales (Callaghan et al., 2024).

Recent technological and methodological advances have greatly expanded the use of camera traps (CTs) as a tool for wildlife monitoring (Rovero et al., 2013; McCallum, 2013). Camera traps are a versatile data-collection tool that can generate photographic detections, suitable for analysis with a wide range of analytical frameworks, including capture-recapture models (e.g. Wearn and Glover-Kapfer, 2019). Using CTs offers several advantages over other data collection methods (reviewed in Wearn and Glover-Kapfer, 2019). They enable continuous monitoring without the need for human presence, which translates into i) minimal disturbance to wildlife (McCallum, 2013), ii) reduced observer bias (Caravaggi et al., 2020); iii) the possibility to collect data for extended periods of time, during day and night, and under variable weather conditions, thus increasing detectability of elusive or nocturnal species (Tan et al., 2013), and iv) the possibility of deployment in remote and difficult-to-access areas. Together, these characteristics contribute to considerably reducing logistical hurdles and monetary costs, which are usually the main limiting factors in large-scale monitoring designs (Sadlier et al., 2004). Moreover, recent advances in automated image processing have made the analysis of camera trap data faster and more standardised (Scotson et al., 2017; Tuia et al., 2022; Vélez et al., 2023), leading to more comprehensive datasets (Kays et al., 2009).

Despite these advantages, turning camera trap data into reliable population estimates is not straightforward (Delisle et al., 2021). A key issue is that not all individuals present in the population are detected, a limitation not unique to camera traps but common across most wildlife monitoring methods (Williams et al., 2002). Statistical models used to derive abundance estimates from camera trap data must therefore explicitly account for imperfect detection (MacKenzie et al., 2002). When individual animals are uniquely identifiable, e.g. when they have been marked or when they present unique coloration patterns like tigers or jaguars, robust statistical methods, like capture-recapture and its extensions, can be used for accurate population size estimation (Royle et al., 2014). Capture-recapture models have been further developed to address heterogeneity in detection probability caused by individual characteristics (i.e., sex or social status), site-specific conditions (Royle et al., 2009; Sollmann et al., 2013), and more recently, spatial heterogeneity in detectability arising from the movement of individuals within the population with Spatial Capture-Recapture models (SCR; Borchers & Efford, 2008; Dorazio & Royle, 2005; Royle & Young, 2008). These developments have consolidated capture-recapture methods as an essential tool for converting individual detection data into reliable estimates of population size, and thus as a cornerstone of modern wildlife monitoring (Royle et al., 2014; Nichols & Williams 2006).

However, the choice of an appropriate modeling framework largely depends on whether individuals can be reliably identified, as this determines the level of complexity and information that can be incorporated into the analysis (Gilbert et al., 2021). For species lacking distinctive, individually unique, and temporally stable markings present across all individuals; alternative models must be considered, such as camera-trap distance sampling (CTDS; Harris et al., 2020; Howe et al., 2017), random encounter models (REM; Rowcliffe et al., 2008), random encounter and staying time models (REST; Nakashima et al., 2020), space-to-event (STE) and time-to-event (TTE) models (Moeller et al., 2018). Unlike capture-recapture approaches, these methods often require additional data beyond capture histories to allow for the estimation of population size. For instance, REST necessitates information on individual movement and speed (Santini et al., 2022); REM requires measurement of the camera's detection area and individual movement speeds (Rowcliffe et al., 2008). CTDS also requires the camera's detection area, as well as a measure of the distance between the animal and the camera trap for each capture (Buckland et al., 2005). Collecting these auxiliary data can be challenging (Rovero and Marshall, 2009; Cusack et al., 2015; Caravaggi et al., 2016), and the underlying assumptions of these models, such as non-random placement of camera traps (Chauvenet et al., 2017), are easily violated. The performance of these methods is thus highly sensitive to the quality of the supplementary data (Santini et al., 2022).

By contrast, Spatial Count models (SC, also known as unmarked spatial capture-recapture; Chandler and Royle, 2013), which derive from the SCR framework, do not require additional data. SC models estimate the distribution of individual activity centres (AC) by analysing spatial recapture data of unmarked animals and determining the scale parameter sigma (σ), which reflects the spatial extent of an individual's movements around its AC (Royle et al., 2014). Although SC models do not require additional data in theory, their reliability has been shown to be highly dependent on species-specific characteristics (e.g. home range size) and camera trap deployment (Burgar et al., 2018; Sun and Burton, 2024). Even in favorable conditions, SC models have been shown to produce imprecise density estimates (Royle et al., 2014; Burgar et al., 2018; Augustine et al., 2019). Together, these factors raise questions about the applicability of SC models for large areas and widespread unmarked species. In this context, Bayesian statistics offer a potential way to mitigate some of these issues by incorporating prior information derived from previous studies or expert knowledge (Gelman and Shalizi, 2012). Indeed, SC models have been shown to be sensitive to the choice of priors, particularly regarding the spatial scale of individual detection by cameras (σ; Burgar et al., 2018).

In this study, we explored the feasibility of analysing large scale camera trap data with SC models to reliably estimate the population size of wolves (*Canis lupus*), a species lacking individually distinctive marks across the entire population. We used data from the wolf monitoring program in the Italian Alpine regions in 2020–2021. Based on wolf pictures from 755 camera-traps distributed across Northern Italy, we compared five different Bayesian SC models with different degrees of complexity with a reference model. Indeed, the availability of robust, independent abundance estimates for this region, obtained during the same period through SCR modeling based on population-level individual genetic identification (Marucco et al., 2023a), allowed us to evaluate and compare the SC results and to assess the impact of incorporating prior information on the accuracy of population size estimates.

2. Materials and methods

2.1. Wolf camera traps data

Camera trapping was used to estimate the wolf population size in the Italian Alps using SC modeling, alongside an independent reference study which used non-invasive genetic sampling (NGS) in the form of scat collection conducted in the same period of 2020–2021 (see Marucco et al., 2023a for details). A total of 755 camera traps were deployed throughout the study area, covering the Italian Alpine regions (Fig. 1). Camera trap sampling was conducted across the area of wolf presence documented in the previous year. The majority of camera traps were opportunistically positioned in areas where the species was considered

present ($n = 711$) and spatially distributed across a 10 × 10 km overlaid reference grid, with at least 1 CT per cell. Camera-trap density reflected local logistical and financial constraints. The same area was concurrently sampled by travelling systematic transects to collect NGS as described in Marucco et al. (2023a). The remaining camera traps ($n = 44$) were positioned in areas where the presence of the species was not yet confirmed. To ensure that the assumption of a closed population was fulfilled (Dupont et al., 2019), and to facilitate comparison with our reference estimate (Marucco et al., 2023a), we considered in the analysis all pictures taken during the designated sampling period of October to April. We removed from the analysis any image classified as C3 under the SCALP (Status and Conservation of the Alpine Lynx Population) criteria (Molinari-Jobin et al., 2012; applied to wolves, Marucco et al., 2023b), meaning they were too blurry to clearly identify a wolf. The number of CT working days was available for parts of the camera traps ($n = 556$), while information about the sampling effort was not available for the rest.

To avoid a violation of the assumption of detection independence due to the same animal entering the field of view of the camera trap more than once, we defined an "event", i.e. a unique wolf encounter, as the presence or detection of an animal within a camera trap field of view (Jumeau et al., 2017), with a minimum interval of 5 min between events to be considered independent (Rolle et al., 2025; Donini et al., 2025; Henrich et al., 2022). As wolves move in packs, we recorded the minimum group size per event from the image sequence and location of individuals moving in and out of the image frame. We then summed the number of individuals detected per event during a day to create camera-trap specific detection histories.

2.2. Spatial count model

SC models share the same underlying structure as SCR models (Royle et al., 2014) and account for variation in detection probability based on the spatial overlap between individual space use and detector placement (e.g., camera traps). A key feature is the estimation of individual activity centres (ACs), representing the centre of their home ranges (Borchers & Efford, 2008; Royle et al., 2014). Both SCR and SC models rely on spatially correlated detections, repeated observations of individuals across different detectors, to infer population size and spatial distribution (Chandler and Royle, 2013).

To estimate individual ACs, SC models (like SCR) rely on a spatial point process that models the individual AC position in the available habitat S:

$$I_h = e^{\beta X_h} \tag{1}$$

where I_h is the point process intensity in habitat grid cell h, $\boldsymbol{X_h}$ is a vector of covariate values for habitat grid cell h, and $\boldsymbol{\beta}$ is the vector of associated coefficients. In our analysis, $\boldsymbol{S}$ was defined as the 5-km resolution grid covering the entire Italian alpine region for a total of 97,700 km^2 (following Marucco et al., 2023a) extended with a 30-km buffer to allow detection of individuals with AC outside the searched area could be detected within it.

Similar to the data augmentation approach used in SCR, a latent variable z is used to describe individual states, where $z_i = 1$ if individual i belongs to the population and $z_i = 0$ if it does not. The state z then follows a Bernoulli distribution with probability ψ, the probability of an individual actually belonging to the population:

$$z_i \sim Bernoulli(\psi) \tag{2}$$

Population size N is then derived as:

$$N = \Sigma_{i=1}^{M} z_i \tag{3}$$

where M is the augmented population size, i.e. an arbitrary number, much larger than the expected population size (M > > N, in this case we used M = 4000).

The number of detections y of individual i at location j and occasion k are then modelled with a Poisson distribution:

$$y_{ijk} \sim Poisson\left(\lambda_{ijk}\right) \tag{4}$$

where λ_{ijk} is the encounter rate for individual i at camera trap j and

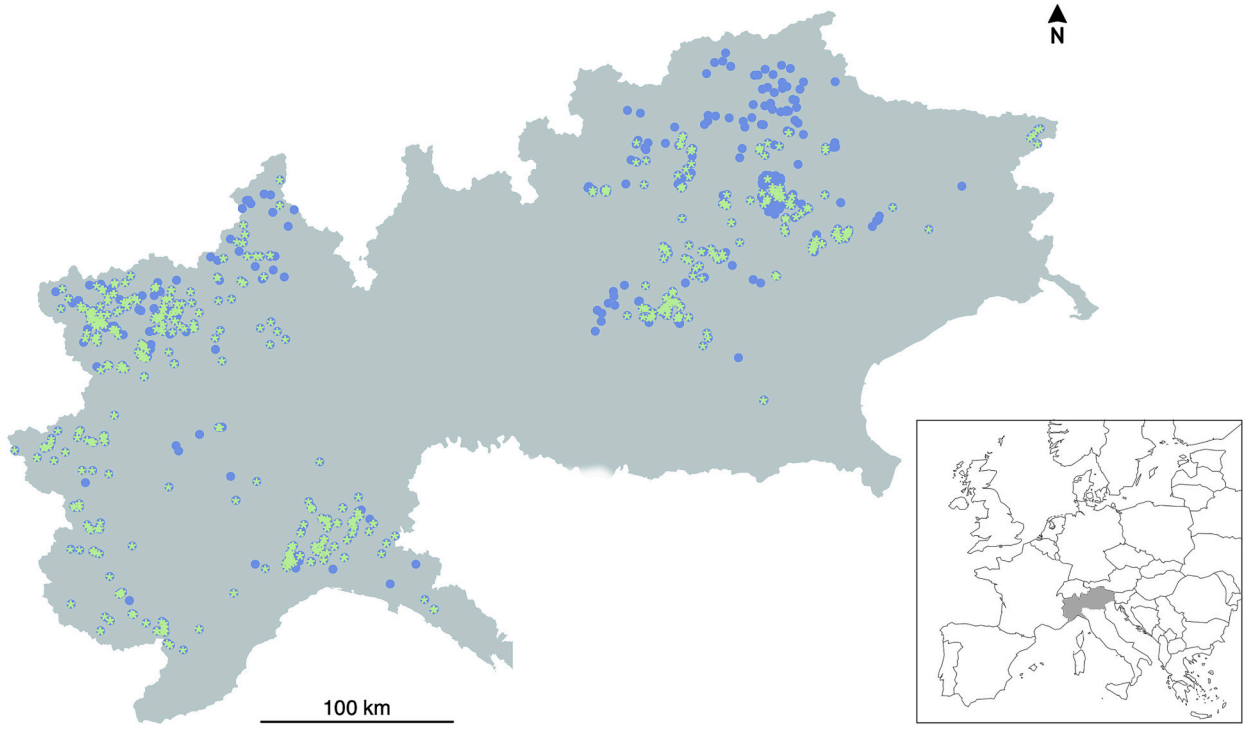

Fig. 1. Map of the camera trap data collected in 2020–2021 in the Italian Alpine region. Blue dots represent camera trap locations and green asterisks indicate wolf encounters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

occasion k. As for SCR, the individual and detector-specific encounter rate can be modelled as a half-normal function, which assumes that the further the camera trap from the activity centre, the lower the probability to detect the individual:

$$\lambda_{ijk} = \lambda_0 exp\left(\frac{-\|s_i - x_j\|^2}{2\sigma^2}\right) z_i \quad (5)$$

where the baseline detection rate (λ_0) represents the expected number of detections at the AC location and the scale parameter (σ) determines the range of the movement of the individual. x_j are the coordinates of trap j and s_i are the coordinates of the AC of individual i. Note the use of z_i to condition the detection of an individual on its presence (z_i=1) in the population.

However, in SC models, and contrary to SCR, individuals are not uniquely identifiable. Thus, only the cumulative number of detections of all individuals at a given camera trap can be recorded. Thanks to the additive properties of the Poisson distribution, Y_j, the overall number of detections recorded at camera trap j can also be expressed as following a Poisson distribution:

$$Y_j \sim Poisson\left(\Lambda_j K_j\right) \quad (6)$$

where, K_j is the number of occasions, i.e. the number of days a camera trap was active in this case, and Λ_j is the overall encounter rate at trap j per occasion across all individuals, i.e. the expected number of detections at camera trap j in one day. Using K_j allows for variation in trapping effort among camera traps during the study period (e.g., different numbers of days of camera trapping). As this information was missing for several cameras ($n = 199$), we treated K_j as a latent variable following a truncated Poisson distribution, constraining the number of active days to be at least one day. This choice was motivated by the unavailability of exact removal dates for a subset of cameras. The Poisson prior was applied consistently across all models.The overall encounter rate Λ_j is obtained by summing over the individual encounter rates:

$$\Lambda_j = \Sigma_{i=1}^{M}\ \lambda_{ij} \quad (7)$$

2.3. Model comparisons

In order to evaluate the performance of SC models to estimate population size for the wolf population in the Italian Alpine region based on camera trap data, we built and compared five different Bayesian Spatial Count models which differed mainly in their use of prior information. Previous studies have discussed the importance of priors for SC models, highlighting how they can significantly influence the model's outcome (Burgar et al., 2018; Gilbert et al., 2021; Twining et al., 2022; Sun and Burton, 2024). We thus used the ability to provide a priori information to the model when estimating parameters in a Bayesian statistics framework to test the influence of providing prior ecological knowledge about the population on the resulting abundance estimates.

One argument commonly raised by practitioners against the use of informative priors, is the difficulty to obtain reliable independent estimates for the parameters of interest (Banner et al., 2020), i.e. parameters that are directly comparable and transferable to the population under study. In our situation, we were able to rely on the results of the SCR model analysis of the NGS data (Marucco et al., 2023a) that was conducted in the same population and during the same period, hence ensuring transferability of the estimated parameters. The analysis of the NGS data using an SCR model led to the first abundance estimate for the wolf population in the Italian Alpine region. Because of the similarity in nature between the two models, the different parameters estimated by the SCR model provided natural priors for the different SC models we wished to compare. Furthermore, we used the same environmental covariates to model the variation in density in the SCR and SC models: Forest cover, Low vegetation cover, Bare Rocks cover, Human Population Density and Wolf Historical Index; see Marucco et al. (2023a) for more details.

We fitted and compared five different models of increasing complexity:

(i) M1 is the null model, with no covariate on density, and uninformative priors on all model parameters. This model represents the baseline scenario in which no prior ecological knowledge about the population is available and no attempt is made to account for spatial variation in density. Here, we assumed a uniform density throughout the study area S, and similar detection parameters for all individuals in the population:

$$\psi \sim Uniform(0, 1) \quad (8)$$

$$\lambda_0 \sim Uniform(0, 100) \quad (9)$$

$$\sigma \sim Uniform(0, 100) \quad (10)$$

(ii) M2 included the five covariates used in the original SCR model to model spatial variation in density, with the goal to test if SC models could identify variation in density like SCR models, and if this affected the final population size estimate. This model represents a scenario in which a practitioner has access to relevant spatial covariates but lacks prior knowledge about the magnitude of their effects on wolf density. Here too, uninformative priors were used:

$$\begin{aligned} \beta_{barerocks} &\sim Normal\ (mean\ = 0, sd = 100) \\ \beta_{lownatveg} &\sim Normal\ (mean = 0, sd = 100) \\ \beta_{forest} &\sim Normal\ (mean = 0, sd = 100) \\ \beta_{human} &\sim Normal\ (mean = 0, sd = 100) \\ \beta_{historic} &\sim Normal\ (mean = 0, sd = 100) \end{aligned} \quad (11)$$

(iii) M3 was similar to M2 but included informative priors on the effect of the covariates on density; this is an idealized scenario in which information about the spatial variation in density in the population is available and can be used directly to inform priors. Priors for the effect of the different covariates were set as normal distributions parametrized using the posterior means and posterior standard deviations from the SCR model:

$$\begin{aligned} \beta_{barerocks} &\sim Normal\ (mean\ = 0.49, sd = 0.41) \\ \beta_{lownatveg} &\sim Normal\ (mean = 2.36, sd = 0.67) \\ \beta_{forest} &\sim Normal\ (mean = -0.45, sd = 0.52) \\ \beta_{human} &\sim Normal\ (mean = -0.67, sd = 0.31) \\ \beta_{historic} &\sim Normal\ (mean = 0.63, sd = 0.06) \end{aligned} \quad (12)$$

(iv) M4 was also similar to M2, but included informative prior on σ, the scale parameter of the detection function. Previous studies showed that SC models struggle to accurately estimate this parameter related to the extent of the space used by an individual in the population, and that providing informative priors for this parameter in particular led to greatly improved population size estimates (Twining et al., 2022). This model represents the more commonly encountered scenario in which no companion SCR study is available, but published estimates of σ from ecologically comparable populations are available in the literature. To mimic this scenario, we conducted a literature search and gathered previously published estimates of σ from SCR analyses of wolf populations in Europe (López-Bao et al., 2018; Mattioli et al., 2018; Jiménez et al., 2023; Gervasi et al., 2024; Iosif et al., 2025; Milleret et al., 2026). Using these values, we parameterized a Gamma distribution to be used as prior for the σ parameter in the SC model:

$$\sigma \sim Gamma(shape = 4.99, scale = 0.13) \quad (13)$$

We additionally present two alternative ways to parameterize the prior distribution for σ in Supplementary Material, one based on the posterior distributions from our reference SCR analysis (Marucco et al., 2023a), and one based on previously published estimates of wolf home-range size estimates.

(v) M5 used strongly informative priors on both space use and population composition in order to try to account for heterogeneity in space use and thus detectability within the population. Wolves are recognized for their robust social structure, as they live in packs (Mech and Boitani, 2003). Within packs, a recognizable familial structure emerges, with two reproducing individuals (RI), pups of different age (offspring), and occasionally dispersers (others), that have different space use and detection probabilities (Marucco et al., 2023a). This model represents the best-case scenario, where highly detailed information about population structure, sex ratios, and individual space use is available from a concurrent SCR analysis. We used different priors for the scale parameters of these different categories, in the form of gamma distributions parameterized using the corresponding posterior values from the reference SCR model:

$$\begin{aligned}\sigma_{f,RI} &\sim Gamma(shape = 259, scale = 0.003)\\ \sigma_{m,RI} &\sim Gamma(shape = 160.11, scale = 0.003)\\ \sigma_{f,offspring} &\sim Gamma(shape = 57.2, scale = 0.04)\\ \sigma_{m,offspring} &\sim Gamma(shape = 194.33, scale = 0.002)\\ \sigma_{f,other} &\sim Gamma(shape = 100, scale = 0.005)\\ \sigma_{m,other} &\sim Gamma(shape = 40.3, scale = 0.14)\end{aligned} \quad (14)$$

We additionally provided prior information about the proportions of each category (sex and status) in the population (θ) using beta distributions, parameterized using the posterior values from the reference SCR model:

$$\begin{aligned}\theta_{f,RI} &\sim Beta(shape = 635.47, scale = 91.95)\\ \theta_{m,RI} &\sim Beta(shape = 68.8, scale = 42.35)\\ \theta_{f,offspring} &\sim Beta(shape = 15.16, scale = 132.61)\\ \theta_{m,offspring} &\sim Beta(shape = 29.79, scale = 71.08)\\ \theta_{f,other} &\sim Beta(shape = 56.68, scale = 35.12)\\ \theta_{m,other} &\sim Beta(shape = 18.53, scale = 193.84)\end{aligned} \quad (15)$$

All prior specifications are provided in Table 1 in Supplementary Information.

2.4. Model fitting and evaluation

We fitted the five SC models using NIMBLE version 0.10.2 (de Valpine et al., 2017) in R version 4.1.3 (R Core Team, 2022). We ran 4 chains of 100,000 iterations each, including a 50,000 burn-in, resulting in a total of 200,000 posterior MCMC samples per model. We assessed model convergence using the Gelman-Rubin diagnostic ($\hat{R} < 1.1$, Gelman & Rubin, 1992) and by visually inspecting traceplots. We evaluated the performance of the different SC models by comparing their estimates of population size N and scale parameter σ to the estimates from the SCR analysis of Marucco et al. (2023a).

3. Results

All Bayesian SC models, with the exception of M5, strongly overestimated population size when compared to the SCR model of Marucco et al. (2023a) (Fig. 2). The naive model, M1, produced a posterior mean estimate N = 2508 individuals (95% CrI 2014-2988). Model M2, in which we considered multiple habitat covariates to explain density variation, displayed a mean posterior estimate of 2779 (95% CrI 2142-3470), also considerably higher than the SCR reference estimate. Providing the model with informative priors on the effect of covariates on population density (M3) reduced the population size estimate to 2346 individuals (CrI 95% 1866-2851). In contrast, using informative priors for σ only, as in model M4, did not result in any decrease in the population size estimate (N = 2961; 95% CrI 2254-3571). Only

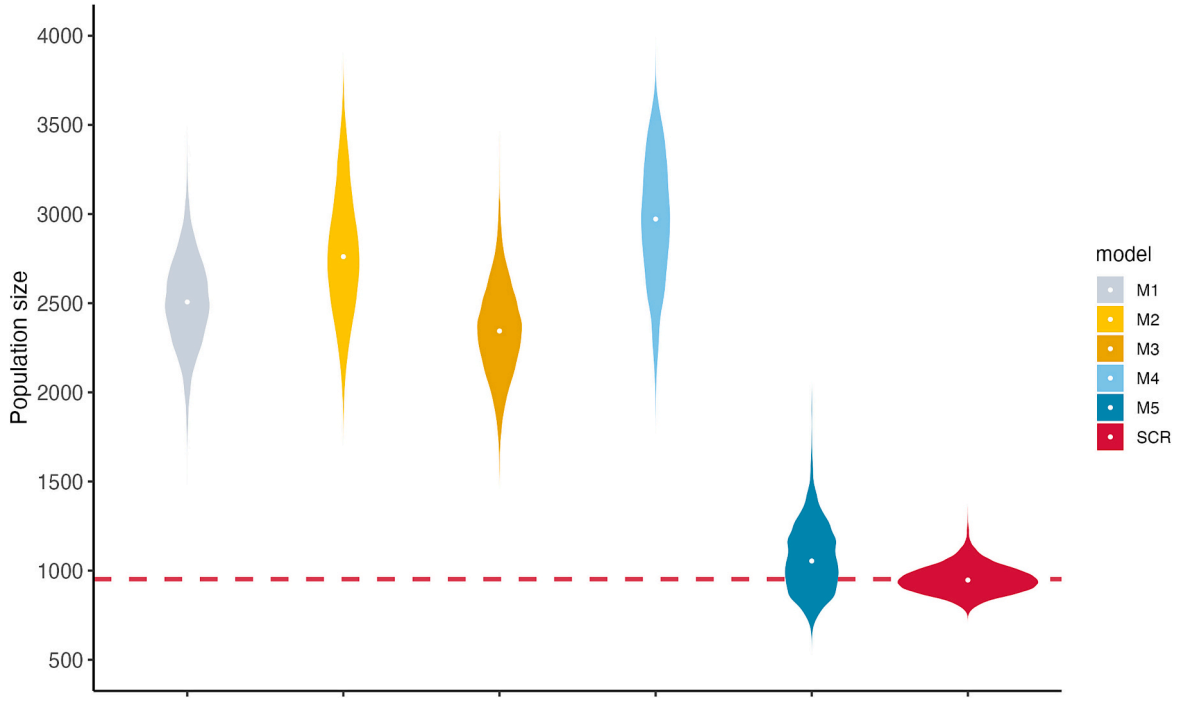

Fig. 2. Posterior distributions of population size N from five different SC models and the SCR from Marucco et al. (2023a), in red, the mean of the SCR model is also represented with a horizontal dashed red line. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

providing highly informative priors on both individual space use and population structure, as in M5, led to a population estimate closer to the reference SCR estimate, reaching 1070 individuals (CrI 95% 764–1449; Fig. 2).

In addition, we observed convergence issues in most cases, as indicated by several parameters with $\hat{R} > 1.1$. Model M5, which more closely approximated the final abundance estimate, displayed the highest number of convergence warnings (Fig. 1, SI). Model M4 and M3 showed better convergence diagnostics but nonetheless failed to produce accurate abundance estimates (Fig. 2).

SC models also provided spatial estimates of density which varied greatly among the models tested (Fig. 3). M1 assumed homogeneous density across the study area. Accordingly, the resulting map shows a relatively homogeneous distribution of individual activity centres, with very limited spatial variation and low to medium wolf density everywhere except in areas with a high density of camera traps. M2, in comparison, allowed density to vary with spatial covariates, with the resulting density surface showing more spatial variation, particularly in the western and central regions (Fig. 3). M3, which used the same covariates as M2 but added informative priors on their effects (based on SCR outputs), displayed even stronger spatial patterns in density, with more distinct high-density regions in the southwest and central zones, but also lower densities in the southern central area corresponding to low elevation regions (Fig. 3). M4, that had informative priors on σ based on other SCR studies, on the other hand, did not show any noticeable difference with M2, and overestimated densities in the low elevation regions compared to the SCR analysis. M5, accounting for within-population heterogeneity (e.g., different detection probabilities and σ for reproducing individuals, offspring and others), produced the density surface that resembled the SCR reference the most, with similarly pronounced high-density areas in the western regions. However, M5 still seemed to overestimate densities in the southern central portion of the study area, with low to medium predicted densities (approx. 0.8–2.0 wolves/100km^2) where the SCR model predicted very low densities (<0.4 wolves/100km^2).

If we consider σ, estimates from SC models that assumed the same value for all individuals (M1 through M4) were very low and similar, around 1 km (Table 1). In M5, even with highly informative priors and considering different σ values for each sex and social status, the model still produced slightly lower estimates than the SCR in some cases (Table 1).

Table 1
Estimates of σ for the different spatial count and reference SCR models (Marucco et al., 2023a). Provided with the mean of the posterior distribution and the relative 95% credibility intervals. Both for the reference sigma and M5 we also provide the different sigma obtained for the different sexes and social statuses (R.I.: reproductive individual, Offspring: individuals associated with an adult couple, Other: individuals not affiliated with a pack).

σ sigma				
Models	Status-sex	2.5% CrI	Mean	97.5% CrI
M1		1.015	1.047	1.151
M2		0.995	1.032	1.22
M3		0.958	0.998	1.11
M4		0.947	0.974	1.087
M5	R.I. ♀	3.29	3.7	4.11
	R.I. ♂	0.68	1.4	2.48
	Offspring ♀	1.64	2.38	2.97
	Offspring ♂	0.76	0.99	1.29
	Other♀	9.32	12.45	15.97
	Other ♂	18.2	26.57	36.69
Marucco et al., 2023a	R.I. ♀	3.2	3.7	4.1
	R.I. ♂	2.1	2.4	2.8
	Offspring ♀	2.5	3	3.5
	Offspring ♂	2.3	2.8	3.4
	Other ♀	22.2	29.6	40.4
	Other ♂	10.6	13.6	17.5

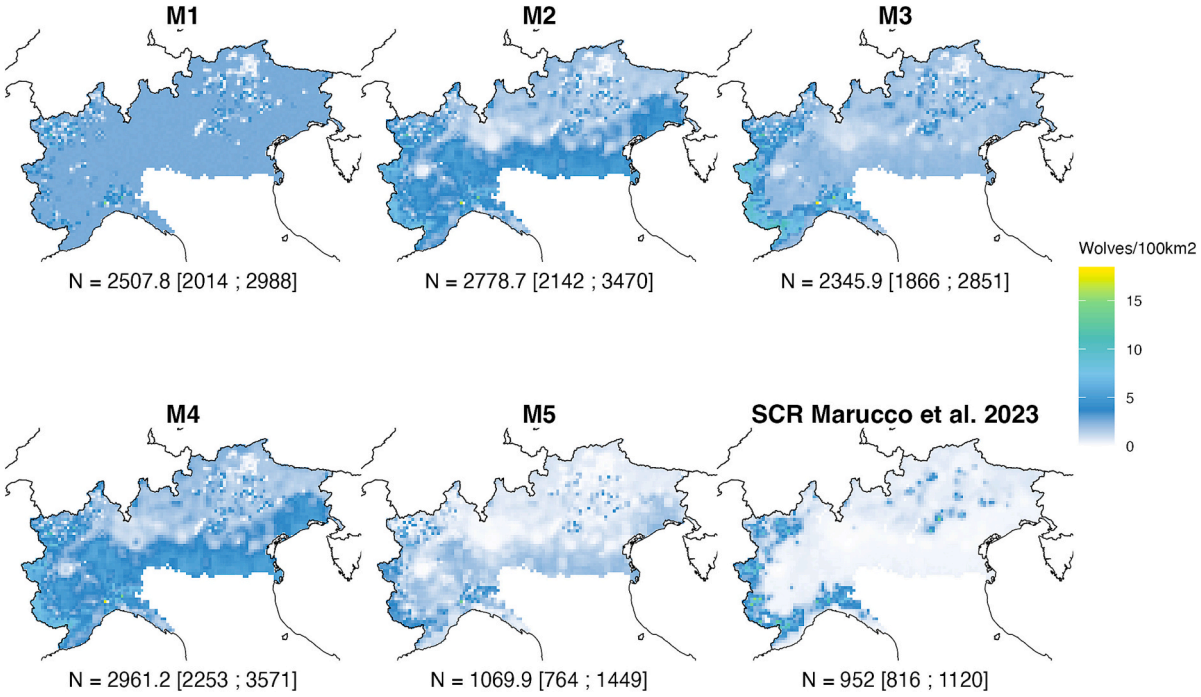

Fig. 3. Density maps from five different SC models and the SCR model from Marucco et al. (2023a). From M1 to M5 the maps highlight the overall decrease in population size as more informative priors are added. In M1 no covariates were considered. In M2 five covariates on density have been considered and in M3 informative priors on the covariate effects have been used in addition. Model M4 and M5 use mildly and strongly informative priors on sigma, the scale parameter. Covariates and informative priors have been obtained from Marucco et al. (2023a), except for M4, where sigma priors have been obtained from published literature on wolves' populations in Europe where SCR have been applied.

4. Discussion

Our results show that using Bayesian spatial count models to estimate large scale abundance of wolves from camera trap data is hardly feasible in practice, unless based on a robust sampling design and supported by highly informative priors. Our study comes as an empirical validation of concerns previously raised about the applicability of SC models to estimate abundance or density in unmarked populations (Royle et al., 2014; Augustine et al., 2018; Augustine et al., 2019; Nakashima et al., 2018; Sun et al., 2022; Martijn et al., 2023; Sun and Burton, 2024). In our study, only model M5, which incorporated highly informative priors on space use and population composition, approached the reference estimate provided by SCR. On the other hand, all other models with non-informative priors, or even models with highly informative priors on space use or density covariates, produced estimates twice as large as our reference.

An important consideration when interpreting these results concerns the meaning of the spatial scale parameter σ across different model types. In our case, σ may differ between the SC models based on CT data and the SCR model based on NGS. These two data types may reflect different aspects of animal space use, which can influence both the magnitude and interpretation of σ in the detection function. Wolves are territorial, and scent-marking activity tends to be concentrated along territory borders (Richardson, 1993). As NGS data typically consists of scats collected throughout the territory, including boundary areas, this may lead to larger σ estimates. In contrast, CTs tend to sample locations where individuals spend more time, often within the core of their home range (Jiménez et al., 2023), which may result in lower σ values due to reduced spatial dispersion in detections. This distinction is particularly relevant for model M5, where convergence issues were most evident in parameters related to the estimation of σ and detection probability (λ_0; Fig. 3, SI). These issues likely stem from the use of informative priors on σ that were inconsistent with the spatial signal in the CT data.

Another aspect regarding σ that must be considered is the fact that SC models are highly sensitive to the choice of its priors (Sun et al., 2014; Burgar et al., 2018; Twining et al., 2022). In our work, it is clear how the choice of priors influenced the final abundance estimates. When the prior distribution for σ was obtained from the literature, we noted a significantly overestimated population size with approximately three times as many individuals as the reference population estimate (Marucco et al., 2023a). We obtained similar results when other data sources were used to inform the prior distribution of σ (see Supplementary Information). In fact, the performance of SC models hinges on the ability to determine individual AC from detection data, which is facilitated when animals are sparsely distributed (low density) and frequently detected (high detectability). Under these conditions, the spatial separation between individuals increases the likelihood that detection patterns can be attributed to distinct ACs, allowing for reliable estimation of σ. In high-density or group-living species, this becomes harder to disentangle due to overlapping and clustering of the detections, which reduces the model's capacity to distinguish individuals and often results in biased estimates of σ and therefore of population size (Sun and Burton, 2024). M1-M4 indeed displayed σ estimates much lower than the SCR ones, and larger abundance estimates, which is consistent with previous simulation studies showing that SC models can produce biased estimates for group-living species where individuals do not move independently (Sun and Burton, 2024).

The poor performance of the different SC models we tested can be also explained by the specific features of the study design, in particular the non-random and opportunistic positioning of CTs. The main challenge with this type of sampling is not so much the use of paths or trails that maximise the probability of detection for wolves (Greco et al., 2025; Jiménez et al., 2023), but rather the spatial coverage of the entire study area by camera traps (Burton et al., 2015; Tobler and Powell, 2013). CTs were placed following a 10 × 10 km grid, but the CT density in a given region reflects, opportunistically, the local logistical and financial constraints. Opportunistic placement of CTs can create gaps in the study area when traps are too far apart (Harmsen et al., 2010; Mccoy et al., 2011; Newey et al., 2015). According to Moqanaki et al. (2021), such spatial gaps in coverage can lead to biased estimates, as the model compensates for unmonitored areas by extrapolating from adjacent data, often assuming uniform density (see e.g. model M1). Most importantly, CTs are often placed where species presence is higher, resulting in a possible correlation between monitoring effort and density of the species monitored across the study area (Brassine and Parker, 2015; Marker et al., 2008). In our case, the dataset lacked cameras in most parts of the study area without confirmed presence of the wolf (Marucco et al., 2023a), which contributed to the overestimation of abundance in models M1 to M4, which estimated higher population densities in these regions compared to the SCR reference (Fig. 3). Including spatial covariates to account for the spatial variation in density resulted in reducing the number of wolves estimated in those most likely unoccupied areas (Fig. 3). However, this alone did not solve the issue. A comparison between M2 and M3, which incorporated informative priors to try and further prevent the model from estimating high densities of wolves in unsuitable areas, showed partial improvement, yet the population size estimate was still far from our reference value. Interestingly, posterior estimates of the effects of spatial covariates on density were significantly different from the SCR estimates, which were used as priors in model M3. In particular, all SC models estimated that wolf density was negatively correlated with forest cover, while the SCR model estimated the opposite effect (Table4, SI). Here too, the absence of a good spatial coverage of the CT distribution might be responsible for this discrepancy. For large-scale population estimates, the adoption of a good sampling design is thus crucial to improve the robustness of SC model results, an issue not limited to SC models but affecting most large-scale monitoring programs where decisions have to be made regarding the distribution of limited resources (Boyd et al., 2023; Irvine et al., 2018; Williams and Brown, 2019). In this context, a stratified random approach to CT allocation could be particularly effective, with strata defined based on expected wolf density: CT density could be higher in areas of higher expected abundance, while ensuring spatially even coverage within each stratum. Specifically, a Generalized Random Tessellation Stratified (GRTS) design could be applied (Stevens and Olsen, 2004) to guide the placement of cameras in clusters, rather than individual camera locations, as adequate spacing and configuration of detector arrays are fundamental for SC and SCR models performances (Sun et al., 2014). Also, it is worth noting that the survey duration was unknown for some cameras, further adding uncertainty in the model. The use of a Poisson distribution to model the latent number of days each camera was active might not adequately capture the variability in search effort and a discrete uniform prior between the day of the last picture and the day the camera was removed could be a more sensible prior. However, this was not feasible in our situation as this information was not available to us.

Another limitation of SC models applied to camera trap data is the assumption that all individuals detected in a given event contribute equally to abundance estimates, i.e. the assumption of independence between individual detections. Since wolves are not individually distinguishable in images because they lack individually distinctive markings that are consistently present across the entire population (transient features such as wounds, occasional markings, or locomotor anomalies are not reliable identifiers as they can be reversed), SC models must rely on aggregated detections. This is particularly problematic for wolves, living in social groups and defending exclusive territories (Mech and Boitani, 2003). Since SC models consider all detections as independent, the simultaneous detection of multiple individuals at the same camera trap location may lead the model to incorrectly assume that they originated from a single individual with high detection probability and small home range. This constraint leads SC models to perform poorly when non-independence between individuals (i.e., aggregation and cohesion, see Bischof et al., 2020) is not addressed, reason why there is

new emergence of models considering clustered detections (Emmet et al., 2022; Meyer et al., 2026). Sun and Burton (2024) showed that SC models are prone to underestimating population size when individuals are spatially clustered. In our case, SC models tended to overestimate abundance, likely reflecting the interaction between opportunistic CT placement and thus large extrapolation across unsampled areas, and unaccounted social aggregation. When information on individual identity (e.g. sex, age class, special marks) is available, Sun et al. (2022) suggested that partial identity models may provide an alternative, leading to reduced bias in abundance estimates, even if such information are usually difficult to collect at large scale. Another avenue would be to further develop SC models to explicitly exploit group-level information inherent in wolf CT data. For territorial, group-living species, the number of individuals detected simultaneously at a given camera location provides a lower bound on local group size and constrains the number of individuals that can plausibly contribute detections in that area. Incorporating this information into the modeling framework (e.g. by estimating the number of individuals within a territory and/or enforcing spatial exclusion among packs could help reduce bias arising from social aggregation and improve the biological realism and performance of SC models.

Further compounding this issue is the challenge of accounting for individual heterogeneity in space use and detection probabilities. Not all individuals are equally detectable, with factors like behaviour, movement patterns, habitat preferences, and social roles influencing detection likelihood (Burton et al., 2022; Caravaggi et al., 2017; Neilson et al., 2018). For wolves, neglecting individual differences in space use and detection probabilities, such as those linked to social status or sex, can result in significant underestimation (Cubaynes et al., 2010). In our study, SC models that assumed homogeneous space use and detection probabilities among individuals in the population (M1–M4), failed to capture population heterogeneity, resulting in overestimation. When individual heterogeneity was incorporated in model M5, performance improved (Figs. 2, 3). However, the use of informative priors alone does not address all underlying methodological challenges; indeed, in this study, we reported diverse convergence issues. It is possible that these issues would have disappeared with longer MCMC chains. Unfortunately, we could not check this by running longer chains given the computational burden of these models. As an example, model M5 took over 2 months on a supercomputer (OCCAM, Aldinucci et al., 2017) to achieve the 100,000 iterations running all four chains in parallel. For that reason alone, the applicability of these models in a large-scale study is debatable.

In addition, the challenges observed may reflect not only sampling design limitations but also data limitations. The absence of individual identity in SC data precludes accounting for any source of heterogeneity in space use or detectability linked with individual characteristics. Without individually observable covariates such as sex or age class, practitioners cannot fit a model with detection parameters stratified by e.g. demographic groups. The reduced resolution of unmarked data thus limits the ability to diagnose and account for such heterogeneity in detectability across individuals in the population, which has been shown to introduce bias in abundance estimates (Sun and Burton, 2024).

5. Conclusion

This study, conducted on a well-studied wolf population across a large spatial scale, highlights the different challenges with obtaining reliable density estimates using SC analysis of large-scale CT data. Our results confirm previous warnings in the literature regarding the practical limitations of SC models, particularly for socially structured and wide-ranging species such as wolves (Sun and Burton, 2024; Augustine et al., 2019). Key improvements are needed to provide reliable estimates with SC models at this scale. First, our results highlight the importance of a good sampling design for large-scale population estimation. Stratified random camera-trap allocation, potentially implemented through a GRTS framework, could improve robustness by concentrating sampling effort in areas of higher expected wolf density while maintaining spatially balanced coverage across the study area. This would however involve deploying a substantially larger number of camera traps to ensure adequate spatial coverage and detection overlap, thus significantly raising costs, to the point of potentially negating the perceived cost advantage of camera trapping over NGS. Burgar et al. (2018) found that, depending on context, NGS can be equally or even more cost-effective than camera trapping, underscoring the need for context-specific evaluations of the trade-off between costs and data, and ultimately inference quality. Second, our study highlights that the reliable application of Bayesian SC models from CT data requires the support of highly informative priors, which are often difficult to obtain. One alternative to balance the cost of NGS used in SCR models and the need for robust prior information in SC models would be to use a hybrid design (see e.g. Gervasi et al., 2024) where only a subset of the study area is monitored using a SCR protocol while CT data is collected in the rest of the study area. An integrated model could then be used to simultaneously estimate the parameters of interest from the SCR model and propagate this information to the SC model. However, caution remains necessary, as SC models are not yet sufficiently developed to reliably handle species with complex social behaviour. Third, new models should be developed to account for group-living and/or territorial species. While, our study does not by itself demonstrate that SC models are broadly unsuitable for wolves or other group-living species, it represents an empirical test that complements existing simulation-based evidence (Sun and Burton, 2024), highlighting the challenges that arise when applying SC models to species with strong social cohesion and non-independent space use, in addition to well-known challenges of large-scale monitoring programs using opportunistic sampling.

In summary, SC analysis of camera-trap data appears not currently suitable for large-scale wolf population size monitoring. Nonetheless, in an adaptive sampling context (Henrys et al., 2024), it is important to keep in mind that the methodology is still evolving and that future developments in both data collection and data analysis methods may lead to more cost-effective and scalable tools for long-term wildlife population assessment in the future.

CRediT authorship contribution statement

M.V. Boiani: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **P. Dupont:** Writing – review & editing, Supervision, Software, Methodology, Funding acquisition, Formal analysis. **R. Bischof:** Writing – review & editing, Resources, Funding acquisition. **O. Friard:** Writing – review & editing, Software. **F. Bisi:** Writing – review & editing, Resources, Data curation. **G. Bombieri:** Writing – review & editing, Resources, Data curation. **S. Calderola:** Writing – review & editing, Resources, Data curation. **S. Carolfi:** Writing – review & editing, Resources, Data curation. **C. Chioso:** Writing – review & editing, Resources, Data curation. **U. Fattori:** Writing – review & editing, Resources, Data curation. **P. Ferrari:** Writing – review & editing, Resources, Data curation. **S. Filacorda:** Writing – review & editing, Resources, Data curation. **P. Molinari:** Writing – review & editing, Resources, Data curation. **L. Corlatti:** Writing – review & editing, Resources, Data curation. **E. Pernechele:** Writing – review & editing, Resources, Data curation. **D. Righetti:** Writing – review & editing, Resources, Data curation. **F. Truc:** Writing – review & editing, Resources, Data curation. **M. Tomasella:** Writing – review & editing, Resources, Data curation. **M. Geary:** Writing – review & editing, Supervision, Methodology, Funding acquisition. **A. von Hardenberg:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition. **E. Avanzinelli:** Writing – review & editing, Resources, Data curation. **F. Marucco:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

The authors thank LIFE Wolfalps EU (LIFE18 NAT/IT/000972, 2020/2024) and LIFE Wild Wolf (LIFE21 NAT/IT/101074417, 2023/2027) for financial support and invaluable contribution to data collection and management. The authors also acknowledge projects WildMap (NFR 286886) and PopFlow (NFR 345279) and the Sustainable Futures PhD scholarship for financial support. We also thank all park rangers, police and forest services, technicians, researchers and volunteers who implemented wolf monitoring. All fieldwork and data collection activities were carried out in accordance with institutional and national guidelines for the ethical treatment of wildlife. The study was also approved by the Ethics Committee of the University of Chester (FSE-REC reference: 193/21/MB/BS) as part of the first author's PhD research project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111988.

Data availability

Scripts are available on GitHub 'https://github.com/PierreDupont/AlpineWolf/tree/main/Analyses/SpatialCount'.

References

Aldinucci, M., Bagnasco, S., Lusso, S., Pasteris, P., Rabellino, S., Vallero, S., 2017. OCCAM: a flexible, multi-purpose andextendable HPC cluster. J. Phys. Conf. Ser. 898, 082039.

Augustine, B.C., Royle, J.A., Kelly, M.J., Satter, C.B., Alonso, R.S., Boydston, E.E., Crooks, K.R., 2018. Spatial capture–recapture with partial identity: an application to camera traps. Ann. Appl. Stat. 12 (1), 67–95. https://doi.org/10.1214/17-AOAS1091.

Augustine, B.C., Royle, J.A., Murphy, S.M., Chandler, R.B., Cox, J.J., Kelly, M.J., 2019. Spatial capture–recapture for categorically marked populations with an application to genetic capture–recapture. Ecosphere 10, e02627.

Banner, K.M., Irvine, K.M., Rodhouse, T.J., 2020. The use of Bayesian priors in ecology: the good, the bad and the not great. Methods Ecol. Evol. 11 (8), 882–889.

Bischof, R., Dupont, P., Milleret, C., Chipperfield, J., Royle, J.A., 2020. Consequences of ignoring group association in spatial capture–recapture analysis. Wildl. Biol. 2020 (1), 1–10.

Bonebrake, T.C., Christensen, J., Boggs, C.L., Ehrlich, P.R., 2010. Population decline assessment, historical baselines, and conservation. Conserv. Lett. 3, 371–378. https://doi.org/10.1111/j.1755-263X.2010.00139.x.

Borchers, D.L., Efford, M.G., 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics 64 (2), 377–385.

Boyd, R.J., Powney, G.D., Pescott, O.L., 2023. We need to talk about nonprobability samples. Trends Ecol. Evol. 38 (6), 521–531.

Brassine, E., Parker, D., 2015. Trapping elusive cats: using intensive camera trapping to estimate the density of a rare African felid. PLoS One 10 (12), e0142508.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 2005. Distance sampling. In: Armitage, P., Colton, T. (Eds.), Encyclopedia of Biostatistics. https://doi.org/10.1002/0470011815.b2a16019.

Burgar, J.M., Stewart, F.E., Volpe, J.P., Fisher, J.T., Burton, A.C., 2018. Estimating density for species conservation: comparing camera trap spatial count models to genetic spatial capture-recapture models. Glob. Ecol. Conserv. 15, e00411.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. REVIEW: wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. 52, 675–685. https://doi.org/10.1111/1365-2664.12432.

Burnham, K.P., Anderson, D.R., Laake, J.L., 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72, 3–202.

Burton, A.C., Beirne, C., Sun, C., Granados, A., Procko, M., Chen, C., Fennell, M., Constantinou, A., Colton, C., Tjaden-McClement, K., Fisher, J.T., Burgar, J., 2022. Behavioral "bycatch" from camera trap surveys yields insights on prey responses to human-mediated predation risk. Ecol. Evol. 12, e9108. https://doi.org/10.1002/ece3.9108.

Callaghan, C.T., Santini, L., Spake, R., Bowler, D.E., 2024. Population abundance estimates in conservation and biodiversity research. Trends Ecol. Evol. 39 (6), 515–523.

Caravaggi, A., Zaccaroni, M., Riga, F., Schai-Braun, S.C., Dick, J.T.A., Montgomery, W.I., Reid, N., 2016. An invasive-native mammalian species replacement process captured by camera trap survey random encounter models. Remote Sensing Ecol. Conserv. 2, 45–58.

Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M., Haswell, P.M., Hayward, M.W., Wood, M.D., 2017. A review of camera trapping for conservation behaviour research. Remote Sens. Ecol. Conserv. 3 (3), 109–122.

Caravaggi, A., Burton, A.C., Clark, D.A., Fisher, J.T., Grass, A., Green, S., Hobaiter, C., Hofmeester, T.R., Kalan, A.K., Rabaiotti, D., Rivet, D., 2020. A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. Conserv. Sci. Pract. 2 (8). https://doi.org/10.1111/csp2.239 (Blackwell Publishing Inc.).

Chandler, R.B., Royle, A.J., 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. Ann. Appl. Stat. 7 (2), 936–954. https://doi.org/10.1214/12-AOAS610.

Chauvenet, A.L., Gill, R.M., Smith, G.C., Ward, A.I., Massei, G., 2017. Quantifying the bias in density estimated from distance sampling and camera trapping of unmarked individuals. Ecol. Model. 350, 79–86.

Cubaynes, S., Pradel, R., Choquet, R., Duchamp, C., Gaillard, J.-M., Leberton, J.-D., Marboutin, E., Miquel, C., Reboulet, A.-M., Poillot, C., Taberlet, P., Gimenez, O., 2010. Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. Conserv. Biol. 24, 621–626. https://doi.org/10.1111/j.1523-1739.2009.01431.x.

Cusack, J.J., Dickman, A.J., Rowcliffe, J.M., Carbone, C., Macdonald, D.W., Coulson, T., 2015. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. PLoS One 10, e0126373.

de Valpine, P., Turek, D., Paciorek, C.J., Anderson-Bergman, C., Lang, D.T., Bodik, R., 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. J. Comput. Graph. Stat. 26 (2), 403–413.

Delisle, Z.J., Flaherty, E.A., Nobbe, M.R., Wzientek, C.M., Swihart, R.K., 2021. Next-generation camera trapping: systematic review of historic trends suggests keys to expanded research applications in ecology and conservation. Front. Ecol. Evol. 9, 617996.

Donini, V., Pedrotti, L., Ferretti, F., Iacona, E., Lorenzetti, L., Cozzi, F., Corlatti, L., 2025. Spatial and temporal relationships between roe and red deer in an Alpine area. Ecol. Evol. 15 (1), e70777. https://doi.org/10.1002/ece3.70777.

Dorazio, R.M., Royle, J.A., 2005. Estimating size and composition of biological communities by modeling the occurrence of species. J. Am. Stat. Assoc. 100 (470), 389–398.

Dupont, P., Milleret, C., Gimenez, O., Bischof, R., 2019. Population closure and the bias-precision trade-off in spatial capture–recapture. Methods Ecol. Evol. 10 (5), 661–672.

Emmet, R.L., Augustine, B.C., Abrahms, B., Rich, L.N., 2022. A spatial capture–recapture model for group-living species. Ecology 103 (10), e3576. https://doi.org/10.1002/ecy.3576.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7 (4), 457–472.

Gelman, A., Shalizi, C.R., 2012. Philosophy and the practice of Bayesian statistics. Br. J. Math. Stat. Psychol. 66 (1), 8–38. https://doi.org/10.1111/j.2044-8317.2011.02037.x.

Gervasi, V., Aragno, P., Salvatori, V., Caniglia, R., De Angelis, D., Fabbri, E., La Morgia, V., Marucco, F., Velli, E., Genovesi, P., 2024. Estimating distribution and abundance of wide-ranging species with integrated spatial models: opportunities revealed by the first wolf assessment in south-central Italy. Ecol. Evol. 14 (5), e11285.

Gilbert, N.A., Clare, J.D.J., Stenglein, J.L., Zuckerberg, B., 2021. Abundance estimation of unmarked animals based on camera-trap data. Conserv. Biol. 35 (1), 88–100. Blackwell Publishing Inc. https://doi.org/10.1111/cobi.13517.

Greco, I., Salvatori, M., Buonafede, E., Pistolesi, A., Corradini, A., Cappai, N., Marconi, M., Seidenari, L., Cagnacci, F., Rovero, F., 2025. Placement matters: implications of trail- versus random-based camera-trap deployment for monitoring mammal communities. Ecol. Appl. 35 (5), e70083. https://doi.org/10.1002/eap.70083.

Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L., Doncaster, C.P., 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize: trail use by Neotropical forest mammals. Biotropica 42, 126–133.

Harris, G.M., Butler, M.J., Stewart, D.R., Rominger, E.M., Ruhl, C.Q., 2020. Accurate population estimation of Caprinae using camera traps and distance sampling. Sci. Rep. 10 (1). https://doi.org/10.1038/s41598-020-73893-5.

Hayne, D.W., 1949. Two methods for estimating population from trapping records. J. Mammal. 30 (4), 399–411.

Henrich, M., Hartig, F., Dormann, C.F., et al., 2022. Deer behavior affects density estimates with camera traps, but is outweighed by spatial variability. Front. Ecol. Evol. 10, 881502. https://doi.org/10.3389/fevo.2022.881502.

Henrys, P.A., Mondain-Monval, T.O., Jarvis, S.G., 2024. Adaptive sampling in ecology: key challenges and future opportunities. Methods Ecol. Evol. 15, 1483–1496. https://doi.org/10.1111/2041-210X.14393.

Howe, E.J., Buckland, S.T., Després-Einspenner, M.L., Kühl, H.S., 2017. Distance sampling with camera traps. Methods Ecol. Evol. 8 (11), 1558–1565. https://doi.org/10.1111/2041-210X.12790.

Iosif, R., Skrbinšek, T., Erős, N., Konec, M., Boljte, B., Jan, M., Promberger-Fürpass, B., 2025. Wolf population size and composition in one of Europe's strongholds, the Romanian Carpathians. Ecol. Evol. 15 (4), e71200.

Irvine, K.M., Rodhouse, T.J., Wright, W.J., Olsen, A.R., 2018. Occupancy modeling species–environment relationships with non-ignorable survey designs. Ecol. Appl. 28 (6), 1616–1625.
Jiménez, J., Daniel, C., García-Dominguez, F., Barasona, J.A., 2023. Estimating wolf (*Canis lupus*) densities using video camera traps and spatial capture–recapture analysis. Ecosphere 14 (7), e4604. https://doi.org/10.1002/ecs2.4604.
Jumeau, J., Petrod, L., Handrich, Y., 2017. A comparison of camera trap and permanent recording video camera efficiency in wildlife underpasses. Ecol. Evol. 7 (18), 7399–7407. https://doi.org/10.1002/ece3.3149.
Kays, R., Kranstauber, B., Jansen, P., Carbone, C., Rowcliffe, M., Fountain, T., Tilak, S., 2009. Camera traps as sensor networks for monitoring animal communities. Proceedings - Conference on Local Computer Networks, LCN, pp. 811–818. https://doi.org/10.1109/LCN.2009.5355046.
Krebs, C.J., 1999. Ecological Methodology, 2nd ed. Addison Wesley Longman, Menlo Park, Calif.
López-Bao, J.V., Godinho, R., Pacheco, C., Lema, F.J., García, E., Llaneza, L., Palacios, V., Jiménez, J., 2018. Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. Sci. Rep. 8 (1), 2177.
Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J., Stuart, S.N., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv. Biol. 22, 1424–1442.
MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8), 2248–2255.
Marker, L.L., Fabiano, E., Nghikembua, M., 2008. The use of remote camera traps to estimate density of free-ranging cheetahs in north-central Namibia. Cat News 49, 22–24.
Martijn, B., Jim, C., Natalie, B., Thomas, N., 2023. Simulation-based assessment of the performance of hierarchical abundance estimators for camera trap surveys of unmarked species. Sci. Rep. 13 (1), 16169.
Marucco, F., Boiani, M.V., Dupont, P., Milleret, C., Avanzinelli, E., Pilgrim, K., Schwartz, M.K., von Hardenberg, A., Perrone, D.S., Friard, O.P., Menzano, A., Bisi, F., Fattori, U., Tomasella, M., Calderola, S., Carolfi, S., Ferrari, P., Chioso, C., Truc, F., Bombieri, G., Pedrotti, L., Righetti, D., Acutis, P.L., Guglielmo, F., Hauffe, H.C., Rossi, C., Caniglia, R., Aragno, P., La Morgia, V., Genovesi, P., Bischof, R., 2023. A multidisciplinary approach to estimating wolf population size for long-term conservation. Conserv. Biol. https://doi.org/10.1111/cobi.14132.
Marucco, F., Reinhardt, I., Avanzinelli, E., Zimmermann, F., Manz, R., Potočnik, H., Černe, R., Rauer, G., Walter, T., Knauer, F., Chapron, G., Duchamp, C., 2023b. Transboundary monitoring of the wolf Alpine population over 21 years and seven countries. Anim. Open Access J. MDPI 13 (22), 3551. https://doi.org/10.3390/ani13223551.
Mattioli, L., Canu, A., Passilongo, D., Scandura, M., Apollonio, M., 2018. Estimation of pack density in grey wolf (*Canis lupus*) by applying spatially explicit capture-recapture models to camera trap data supported by genetic monitoring. Front. Zool. 15 (1), 38.
McCallum, J., 2013. Changing use of camera traps in mammalian field research: habitats, taxa and study types. Mammal Rev. 43 (3), 196–206. Blackwell Publishing Ltd. https://doi.org/10.1111/j.1365-2907.2012.00216.x.
Mccoy, J.C., Ditchkoff, S.S., Steury, T.D., 2011. Bias associated with baited camera sites for assessing population characteristics of deer. J. Wildl. Manag. 75, 472–477.
Mech, L.D., Boitani, L., 2003. Wolves: Behavior, Ecology, and Conservation. Univ. of Chicago Press.
Meyer, C.J., Whittington, J., Tourani, M., Hebblewhite, M., 2026. A novel generalized spatial mark-resight model that accounts for group associations. Methods Ecol. Evol. 17, 1275–1289. https://doi.org/10.1111/2041-210x.70271.
Milleret, C., Duchamp, C., Bauduin, S., Kaerle, C., Pirog, A., Queney, G., Gimenez, O., 2026b. Estimating wolf population size in France using non-invasive genetic sampling and spatial capture-recapture models. Biol. Conserv. 317, 111772.
Moeller, A.K., Lukacs, P.M., Horne, J.S., 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. Ecosphere 9 (8). https://doi.org/10.1002/ecs2.2331.
Molinari-Jobin, A., Kery, M., Marboutin, E., Molinari, P., Koren, I., Fuxjager, C., Breitenmoser-Würsten, C., Wölfl, S., Fasel, M., Kos, I., Wölfl, M., Breitenmoser, U., 2012. Monitoring in the presence of species misidentification: the case of the Eurasian lynx in the Alps. Anim. Conserv. 15, 266–273.
Moqanaki, E.M., Milleret, C., Tourani, M., Dupont, P., Bischof, R., 2021. Consequences of ignoring variable and spatially autocorrelated detection probability in spatial capture-recapture. Landsc. Ecol. 36 (10), 2879–2895.
Nakashima, Y., Fukasawa, K., Samejima, H., 2018. Estimating animal density without individual recognition using information derivable exclusively from camera traps. J. Appl. Ecol. 55 (2), 735–744. https://doi.org/10.1111/1365-2664.13059.
Nakashima, Y., Hongo, S., Akomo-Okoue, E.F., 2020. Landscape-scale estimation of forest ungulate density and biomass using camera traps: applying the REST model. Biol. Conserv. 241, 108381. https://doi.org/10.1016/J.BIOCON.2019.108381.
Neilson, E.W., Avgar, T., Burton, A.C., Broadley, K., Boutin, S., 2018. Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. Ecosphere 9, e02092.
Newey, S., Davidson, P., Nazir, S., Fairhurst, G., Verdicchio, F., Irvine, R.J., et al., 2015. Limitations of recreational camera traps for wildlife management and conservation research: a practitioner's perspective. Ambio 44, 624–635.
Nichols, J.D., 2014. The role of abundance estimates in conservation decision-making. In: Verdade, L., Lyra-Jorge, M., Piña, C. (Eds.), Applied Ecology and Human Dimensions in Biological Conservation. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-54751-5_8.
Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends in ecology & evolution 21 (12), 668–673.
R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Richardson, P.R.K., 1993. The function of scent marking in territories: a resurrection of the intimidation hypothesis. Trans. R. Soc. S. Afr. 48 (2), 195–206. https://doi.org/10.1080/00359199309520270.
Rolle, F., Boiani, M.V., Fardone, L., Gaydou, F., Macario, M., Parentela, F., Ruco, V., Sigaudo, D. and, Marucco, F., 2025. Integrating human and wildlife dynamics in co-occurrence modelling. Ecol. Evol. 15, e70984. https://doi.org/10.1002/ece3.70984.
Rovero, F., Marshall, A.R., 2009. Camera trapping photographic rate as an index of density in forest ungulates. J. Appl. Ecol. 46, 1011–1017.
Rovero, F., Zimmermann, F., Berzi, D., Meek, P., 2013. "Which camera trap type and how many do I need?" a review of camera features and study designs for a range of wildlife research applications. Hystrix Ital. J. Mammal. 24 (2), 148–156. https://doi.org/10.4404/hystrix-24.2-8789.
Rowcliffe, J.M., Field, J., Turvey, S.T., Carbone, C., 2008. Estimating animal density using camera traps without the need for individual recognition. J. Appl. Ecol. 45 (4), 1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x.
Royle, J.A., Chandler, R.B., Sollman, R., Gardner, B., 2014. Spatial Capture-Recapture. Elsevier, Oxford, United Kingdom.
Royle, J.A., Nichols, J.D., Karanth, K.U., Gopalaswamy, A.M., 2009. A hierarchical model for estimating density in camera-trap studies. J. Appl. Ecol. 46 (1), 118–127.
Royle, J.A., Young, K.V., 2008. A hierarchical model for spatial capture–recapture data. Ecology 89 (8), 2281–2289.
Sadlier, L.M.J., Webbon, C.C., Baker, P.J., Harris, S., 2004. Methods of monitoring red foxes *Vulpes vulpes* and badgers *Meles meles*: are field signs the answer? Mammal Rev. 34 (1–2), 75–98. https://doi.org/10.1046/j.0305-1838.2003.00029.x.
Santini, G., Abolaffio, M., Ossi, F., Franzetti, B., Cagnacci, F., Focardi, S., 2022. Population assessment without individual identification using camera-traps: a comparison of four methods. Basic Appl. Ecol. 61, 68–81. https://doi.org/10.1016/j.baae.2022.03.007.
Schwarz, C.J., Seber, G.A.F., 1999. Estimating animal abundance: review III. Stat. Sci. 14, 427–456.
Scotson, L., Johnston, L.R., Iannarilli, F., Wearn, O.R., Mohd-Azlan, J., Wong, W.M., Gray, T.N.E., Dinata, Y., Suzuki, A., Willard, C.E., Frechette, J., Loken, B., Steinmetz, R., Moßbrucker, A.M., Clements, G.R., Fieberg, J., 2017. Best practices and software for the management and sharing of camera trap data for small and large scales studies. Remote Sens. Ecol. Conserv. 3 (3), 158–172. Wiley-Blackwell. https://doi.org/10.1002/rse2.54.
Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters, 2nd edn. Griffin, London.
Sollmann, R., Mohamed, A., Samejima, H., Wilting, A., 2013. Risky business or simple solution–relative abundance indices from camera-trapping. Biol. Conserv. 159, 405–412. https://doi.org/10.1016/j.biocon.2012.12.025.
Stevens, D.L., Olsen, A.R., 2004. Spatially balances sampling of nature resources. J. Am. Stat. Assoc. 99, 262–278.
Sun, C., Burton, A.C., 2024. The importance of independence in unmarked spatial capture–recapture analysis. Wildl. Biol., e01182 https://doi.org/10.1002/wlb3.01182.
Sun, C.C., Fuller, A.K., Royle, J.A., 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PLoS One 9, e88025.
Sun, C., Burgar, J.M., Fisher, J.T., Burton, A.C., 2022. A cautionary tale comparing spatial count and partial identity models for estimating densities of threatened and unmarked populations. Glob. Ecol. Conserv. 38. https://doi.org/10.1016/j.gecco.2022.e02268.
Tan, C.L., Yang, Y., Niu, K., 2013. Into the night: camera traps reveal nocturnal activity in a presumptive diurnal primate, *Rhinopithecus brelichi*. Primates 54 (1), 1–6. https://doi.org/10.1007/s10329-012-0318-2.
Tobler, M.W., Powell, G.V., 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. Biol. Conserv. 159, 109–118.
Tuia, D., Kellenberger, B., Beery, S., Costelloe, B.R., Zuffi, S., Risse, B., Mathis, A., Mathis, M.W., van Langevelde, F., Burghardt, T., Kays, R., Klinck, H., Wikelski, M., Couzin, I.D., van Horn, G., Crofoot, M.C., Stewart, C.V., Berger-Wolf, T., 2022. Perspectives in machine learning for wildlife conservation. Nat. Commun. 13 (1). https://doi.org/10.1038/s41467-022-27980-y. Nature Research.
Twining, J.P., McFarlane, C., O'Meara, D., O'Reilly, C., Reyne, M., Montgomery, W.I., Helyar, S., Tosh, D.G., Augustine, B.C., 2022. A comparison of density estimation methods for monitoring marked and unmarked animal populations. Ecosphere 13 (10), e4165. https://doi.org/10.1002/ecs2.4165.
Vélez, J., McShea, W., Shamon, H., Castiblanco-Camacho, P.J., Tabak, M.A., Chalmers, C., Fergus, P., Fieberg, J., 2023. An evaluation of platforms for processing camera-trap data using artificial intelligence. Methods Ecol. Evol. 14 (2), 459–477.
Wearn, O.R., Glover-Kapfer, P., 2019. Snap happy: camera traps are an effective sampling tool when compared with alternative methods. R. Soc. Open Sci. 6 (3). https://doi.org/10.1098/rsos.181748.
Wiewel, A.S., Adams, A.A.Y., Rodda, G.H., 2009. Evaluating abundance estimate precision and the assumptions of a count-based index for small mammals. J. Wildl. Manag. 73, 761–771. https://doi.org/10.2193/2008-180.
Williams, B.K., Brown, E.D., 2019. Sampling and analysis frameworks for inference in ecology. Methods Ecol. Evol. 10 (11), 1832–1842.
Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press.