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Note

Abundance of Rare and Elusive Species: Empirical Investigation of Closed Versus Spatially Explicit Capture–Recapture Models With Lynx as a Case Study

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ABSTRACT Effective conservation and management require reliable monitoring methods and estimates of abundance to prioritize human and financial investments. Camera trapping is a non-invasive sampling method allowing the use of capture–recapture (CR) models to estimate abundance while accounting for the difficulty of detecting individuals in the wild. We investigated the relative performance of standard closed CR models and spatially explicit CR models (SECR) that incorporate spatial information in the data. Using simulations, we considered 4 scenarios comparing low versus high detection probability and small versus large populations and contrasted abundance estimates obtained from both approaches. Standard CR and SECR models both provided minimally biased abundance estimates, but precision was improved when using SECR models. The associated confidence intervals also provided better coverage than their non-spatial counterpart. We concluded SECR models exhibit better statistical performance than standard closed CR models and allow for sound management strategies based on density maps of activity centers. To illustrate the comparison, we considered the Eurasian lynx (*Lynx lynx*) as a case study that provided the first abundance estimates of a local population in France.

KEY WORDS abundance, camera trapping, capture–recapture models, *Lynx lynx*, relative bias, root mean square error, simulations, spatially explicit.

The presence of large carnivores (wolves, bears, lynx, and wolverines) usually results in strong socio-cultural issues in all societies, Europe being no exception. These species share common features such as large territories and the need for a large mosaic of habitat and prey, potentially competing with human activities (e.g., hunting and raising livestock). Such conflicts, in combination with habitat loss, have led to local extirpation of large carnivores in many areas. Although large carnivores were almost extinct at the beginning of the 20th century in many European countries, their populations have slowly recovered via reintroduction or natural re-colonization through dispersal.

In this context, the Bern Convention (1979), the European Habitats Directive (1992), and the International Union for Conservation of Nature (IUCN) Red list provided specific indices and rules to assess the conservation status of species and to help assess how management decisions could meet the conservation requirements. Abundance was defined as one of the key estimates needed in assessing species' statuses. Moreover, it is the state variable of interest in most ecological research and monitoring programs involving management and conservation of animal populations (Nichols and MacKenzie 2004). Indeed, reliable estimates of population size are essential to evaluate conservation and wildlife management programs, such as reintroduction programs. However, large carnivores are difficult to monitor because they are elusive, live at low densities over wide areas, and are usually solitary and mostly nocturnal. Exhaustive counts are therefore often expensive, time consuming, and sometimes impractical.

To assess population trends in elusive and wide-ranging species, non-invasive survey methods have been used increasingly over the last decade. In particular, camera-trapping methods combined with capture–recapture (CR) modeling

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have become a standard tool to estimate carnivore abundance while accounting for detectability <1 (e.g., tigers [*Panthera tigris*]: Karanth et al. 2006, Karanth and Nichols 1998; ocelots [*Felis pardalis*]: Trolle and Kéry 2003; snow leopards [*Uncia uncia*]: Jackson et al. 2006; jaguars [*Panthera onca*]: Silver et al. 2004). Standard CR models usually assume geographical closure (no movement in or off the sampling grid). However, this assumption is often violated, especially for mammals with large home ranges. Another major assumption of these models is that no individual within the sampled area has a zero probability of being captured. To address these issues, an alternative approach known as spatially explicit CR modeling (SECR) was developed recently (Royle and Young 2008, Borchers and Efford 2008). This method has been applied to a large number of taxa (e.g., birds: Efford 2004, Borchers and Efford 2008, Efford et al. 2009*a*; cetaceans: Marques et al. 2012; stoats: Efford et al. 2009*b*; bears: Obbard et al. 2010, and lizards: Royle and Young 2008). In SECR models, the probability of detection for each trap is modeled as a function of distance between a latent variable, the individual activity center (equivalent to the home range center) from which animals move randomly, and the camera trap where they have been captured. This model does not rely on the assumption of geographic closure by accounting for the fact that animals move and that detection probability depends on their center of activity (Gardner et al. 2009).

Our objectives were twofold. First, we aimed at evaluating the relative performance of SECR methods versus conventional non-spatial CR models in estimating abundance in the context of carnivore conservation. Most of the studies assessing bias in spatial models compared abundance estimates using real datasets rather than simulated data, hence were unable to infer bias and precision (e.g., Gardner et al. 2009). Recent papers dealing with SECR models and simulations (Efford 2004, 2011; Borchers and Efford 2008; Royle and Young 2008) focused on the performance of different methods to estimate density (e.g., nested subgrid vs. inverse prediction, frequentist vs. Bayesian methods) but did not formally compare SECR and non-spatial models. Therefore, we carried out a simulation study with several scenarios comparing low versus high detection probability and small versus large populations to quantify the performances of parameter estimates using both SECR and non-spatial models. We also suggested how the simulation results could be used to improve the trapping design when necessary. Second, we used the 2 methods to analyze a real dataset from a camera-trapping experiment with the Eurasian lynx (*Lynx lynx*) in the French Jura Mountains. This population originates from reintroductions in Switzerland in the 1970s. Although listed as a species of Least Concern given its wide range (IUCN 2001), habitat loss, prey depletion, and poaching are still regarded as potential threats. Up to now, the main monitoring program for lynx in France was based on indirect signs (i.e., tracks, scat, hair, and other signs) collected by a network of volunteers (state employees, hunters, naturalists, farmers, and mountain guides). Although the use of indirect signs is often the most effective and least expensive method for estimating the distribution of carnivores, the resulting estimates of population parameters, such as abundance, are often approximate. Camera-trap monitoring has recently been initiated in France to monitor the lynx population and evaluate the conservation status of a population where problematic interactions between hunters and lynx exist. We provided the first estimate of lynx abundance for this French population. Finally, recommendations are provided for the conservation of elusive species, with an emphasis on large carnivores and their monitoring.

STUDY AREA

Our study area was located in a 480-km^2 zone in the southern center of the French department of Jura between the Vouglans lake and the southern border of Doubs department. We delimited this study area using knowledge on lynx habitat and forest continuity.

METHODS

Simulation Study Design

We assumed that our population was demographically and geographically closed (i.e., no birth, death, immigration, or emigration during the sampling period) when applying CR models to estimate abundance. Lynx are long-lived animals (Sunquist and Sunquist 2002) and the camera-trap sampling period was short enough so that we assumed no deaths or births occurred during this period. In addition, the trapping session was timed outside the dispersal period for subadults.

To compare the performance of the standard versus the SECR methods in estimating abundance, we simulated 100 datasets with a particular spatial organization. We considered 4 scenarios comparing low versus high detection probability and small versus large populations. We used these scenarios to evaluate relative bias in parameter estimates and the precision and the coverage of 95% confidence and credible intervals (CI hereafter for Bayesian credible intervals or frequentist confidence intervals, indistinctively). We created each dataset using the trap configuration from monitoring of lynx in the study area (see case study below), but we did not use any constraints to mimic lynx behavior in the simulated datasets. We set the number of capture occasions to $k = 15$ and the actual population size to $N = 10$ or $N = 50$, depending on the scenario. We based the simulations on the SECR model formulation. We simulated the coordinates of N individual activity centers. Then, we evaluated whether we could reliably model a posteriori the number and location of activity centers we had simulated. We conducted the simulation in 2 steps. First, a point process component described the spatial distribution of the centers of activity. Second, an observation process component made the connection between the detection of an individual and its center of activity given the spatial distribution of traps.

Point process.—We assumed a fixed and known number of activity centers s_i (similar to home range centers) with geographic coordinates $s_i = (s_{xi}, s_{yi})$ for each individual i ($i = 1, \dots, N$) of the population. We assumed that these centers of activity were uniformly distributed over a region S, an arbitrary polygon containing the trapping array.

$$s_i \sim \mathrm{Uniform}(S) \tag{1}$$

To simulate capture histories, we assumed that the capture probability of each individual was a function of the distance between its activity center and the trap.

Exposure to traps.—The exposure of an individual to a given trap was a decreasing function of the distance from the activity center to that trap: the further the activity center was from the trap, the less likely the animal was exposed to capture. Thus, we first defined a distance matrix $D_{i,j}$ as the Euclidean distance between every activity center i and trap j:

$$D_{i,j} = \sqrt{(s_{xi} - x_j)^2 + (s_{yi} - y_j)^2} \tag{2}$$

Second, we modeled the exposure of each individual as a function of distance and 2 other parameters:

$$E0_{i,j} = \lambda_0 \exp\left(\frac{-D_{i,j}^2}{\sigma}\right) \tag{3}$$

where λ_0 is the baseline encounter rate (i.e., the expected no. of captures of individual i at trap j during a sampling occasion when an individual's activity center s_i is located precisely at trap j) and parameter σ (in km) controls the shape of the distance function, reflecting how fast the exposure decreases with distance. The greater σ is, the faster the exposure decreases with distance.

Capture process.—If an individual i is exposed to trap j, we assumed a capture probability $p_{i,j}$. The distance function allows the development of the capture process model. The increase of the exposure to traps translates into an increase of the capture probability and was modeled with an exponential function:

$$p_{i,j} = 1 - \exp(-E0_{i,j}) \tag{4}$$

We assigned 2 different values for λ_0 (0.03 and 2) and 1 value to σ (1.5) depending on the scenario. We tested all combinations of all levels of N, λ_0, and σ resulting in 4 scenarios. For each scenario and each simulated dataset, we constructed the distance matrix $D_{i,j}$ between the simulated activity centers and the trap locations. We used the distance matrix to estimate for each individual a per trap capture probability $p_{i,j}$. Then, we performed a binomial trial with parameters N and $p_{i,j}$ to determine whether the individual was captured or not. Since detection is not perfect, only n out of the N total individuals from the population were detected. We compiled for each of the j traps the number of occasions, k, an individual, i, was detected. Thus, for each trap and each individual, a number ranging from 0 to k indicated how many occasions each individual was captured. We used these count histories to fit SECR models. Finally, we analyzed the capture histories of the n individuals under the standard and SECR models.

Model Formulation

Standard CR models.—We first calculated abundance estimates by accounting for detection probabilities using standard CR models. We considered different sources of variation in capture probabilities. In addition to a model with no variation in the detection probability (model M_0), we considered behavioral responses to trapping (model M_b), differences in capture probabilities over time (model M_t), and the most complex models included among-individual heterogeneity in capture probabilities (model M_h; Otis et al. 1978, Williams et al. 2002). In addition, we considered 4 models that were combinations of these sources of variation (Models M_{bh}, M_{th}, M_{tb}, and M_{tbh}). For each simulated dataset, we used Akaike's Information Criterion (AIC) to select the model (Burnham and Anderson 2002). When ΔAIC was <2, the given model is suggested to be within the range of plausible models to best fit the observed data. We conducted analyses via maximum likelihood with the R package Rcapture (Baillargeon and Rivest 2007).

SECR model implementation using a Bayesian approach.—Each camera trap reflected the location of capture, which, in turn, provided insight into the activity center coordinates of each lynx. The SECR model has the advantage of incorporating spatial heterogeneity while estimating abundance (Royle et al. 2009*a*, *b*, 2011). More specifically, the SECR model makes explicit the distinction between 1) a latent component for the spatial point process of the (unknown) location of the activity centers (eqs. 1 and 2) and 2) an observation component that describes how the observed data arise from the point process (eq. 4).

We adopted a Bayesian approach (McCarthy 2007) to fit the SECR model; activity centers were treated as random effects, which are relatively easy to incorporate in the Bayesian framework (King et al. 2009). The Bayesian approach combines the likelihood with prior probability distributions of the parameters to obtain the posterior distribution of the parameters of interest based on Bayes' theorem. We used Markov Chain Monte Carlo (MCMC) methods to simulate observations from the posterior distributions. Regarding priors for parameters, we considered that we did not have any information about the spatial distribution of the activity centers of the simulated individuals, thus we assumed they were uniformly distributed over S. We chose a Uniform(0, 15) distribution for σ and we assigned a Gamma(0.1, 0.1) distribution to λ_0.

To obtain an estimate of abundance, we used a data augmentation approach (Royle and Young 2008). We augmented the data set with 100 individuals and we associated a latent indicator, z_i, with every individual. The encounter histories of the 100 individuals initially contained only zeroes. Some of these individuals were not captured during the intensive camera trapping but belonged to the population. The z_i indicator reflects the probability, Ψ, of an individual to be a member of the population. We assumed a Uniform(0, 1) prior for Ψ. We defined z_i as a binary variable equal to 0 when the individual i was not a member of the population and 1 otherwise. We obtained the abundance, N, as a derived parameter by adding all the presence indicators, z_i. We implemented these analyses in WinBUGS (Spieghalter et al. 2003) called from R using package R2WinBUGS (Sturtz et al. 2005).

Evaluating the performance of the 2 methods.—We evaluated the performance of the standard CR models and the SECR models by comparing the abundance estimates obtained from the 2 methods to the true value of abundance. As a result, we were able to quantify the potential bias in parameter estimates obtained for both models. We looked at the relative bias in $\hat{N}$, the estimator of N, calculated as $(E[\hat{N}] - N)/N$ where the numerator can be approximated as the average over the 100 iterations of the difference between the estimated abundance under the model considered and the true parameter value, $\sum_{i=1}^{100} \hat{N}_i/100 - N$. To assess the precision, we calculated the root mean square error (RMSE) as $\sqrt{E(([\hat{N}] - N)^2)} \approx \sqrt{\sum_{i=1}^{100} (\hat{N}_i - N)^2/100}$. A low RMSE is characteristic of a good trade-off between low bias and high variance. Finally, we looked at the 95% confidence interval coverage by determining and averaging over all simulations whether the interval contained the true value.

Eurasian Lynx in French Jura Mountains

The Eurasian lynx is a solitary nocturnal species, living in forested areas. It can be individually identified based on the photographs of unique pelage patterns (e.g., Zimmermann and Breitenmoser 2007). To maximize detectability, camera traps were set at optimal locations (on game path, hiking trail, forest road) based on previous signs of lynx presence and on local knowledge. In theory, all individuals should have a non-null detection probability to use standard capture–recapture models (Karanth and Nichols 1998), but this requirement is not necessary for SECR models (Royle et al. 2009*a*). Thus, the study area was divided into a grid of 2.7 km × 2.7 km cells (Zimmermann et al. 2007) where 1 of 2 cells was sampled, leading to 33 cells sampled from February to April 2011. This grid size and sampling design ensured that at least 1 camera trap site was set in each potential lynx home range. At each trapping site, 2 camera traps with infrared trigger mechanisms were set to photograph both flanks of the animal, allowing a high level of confidence in individual identification. Date, time, and location of each photographic capture of a lynx were recorded. Camera traps were checked weekly to change memory cards and batteries. The sampling period was divided into 15 occasions, 1 occasion being defined as 4 successive trap nights. We used the results of the SECR model to build a density map of the lynx activity centers. For each of the MCMC iterations, we plotted the centers of activity of the individuals belonging to the population ($z_i = 1$) on successive layers. For every layer, we divided the region S into squares of 500 m × 500 m then we calculated the mean number of activity centers falling into each square. R and WinBUGS codes are available on request from the first author.

RESULTS

Simulation to Compare Spatial Versus Non-Spatial Models

For each scenario and each simulated dataset, we reported the abundance posterior median estimate and its 95% credible interval for the SECR model and the abundance point estimate with its 95% confidence interval from the non-spatial model (Fig. 1). Scenario A represented a small population with a low detection probability mimicking the Eurasian lynx dataset. Both models similarly slightly overestimated abundance; the non-spatial model displayed a relative bias of 0.096 and the SECR model relative bias was 0.121. Scenario B represented a large population with a low detection probability. The non-spatial model clearly underestimated the population size with a relative bias of −0.08, whereas the SECR model slightly underestimated it with a −0.016 relative bias. Scenario C corresponded to a small population with a high detection probability. For most datasets, the non-spatial model provided estimates close to the actual abundance (relative bias around 0.007) but with large confidence intervals and the SECR model provided unbiased estimates (relative bias around −0.02) and small credible intervals. Finally, scenario D represented an ideal situation with a large population and a high detection probability. The non-spatial model slightly overestimated abundance (relative bias = 0.026), whereas the SECR model provided values close to the actual abundance (relative bias = 0.0002). The RMSE clearly revealed that the SECR model provided a better balance between bias and variance for all scenarios than the non-spatial model. The confidence interval of the non-spatial model included the true abundance value in only 73–78 out of the 100 simulated datasets depending on the scenario. The credible interval of the SECR model included the true value in 92–99 datasets (Table 1). Credible intervals of the SECR model provided better coverage than confidence intervals as provided by standard closed CR models.

Lynx Case Study

Data were collected between February and April 2011 from 33 trap sites resulting in 1,980 trap nights. One site was found effective during less than 50% of the trapping nights; therefore, we removed it from the analysis reducing the theoretical effort to 1,816 effective trapping nights. The study provided an encounter history for 9 individuals that were photographed on 14 of the 32 trap sites. Individuals were captured on up to 6 different sites and the maximum distance moved by 1 individual between captures was 27.6 km. Model selection ranked the model incorporating individual heterogeneity in capture probability as the best model (AIC weight = 0.39) followed by the model assuming constant capture probability (ΔAIC = 1.47, AIC weight = 0.22). The Akaike weight of all other models was <0.09. Average estimated detection was 0.14 and the estimated abundance using the best model was 12 individuals (95% CI: 7.14–20.27). For the SECR model, the baseline encounter rate at a given camera (λ_0) was 0.05 photographs/occasion (95% CI: 0.03–0.15); the movement parameter

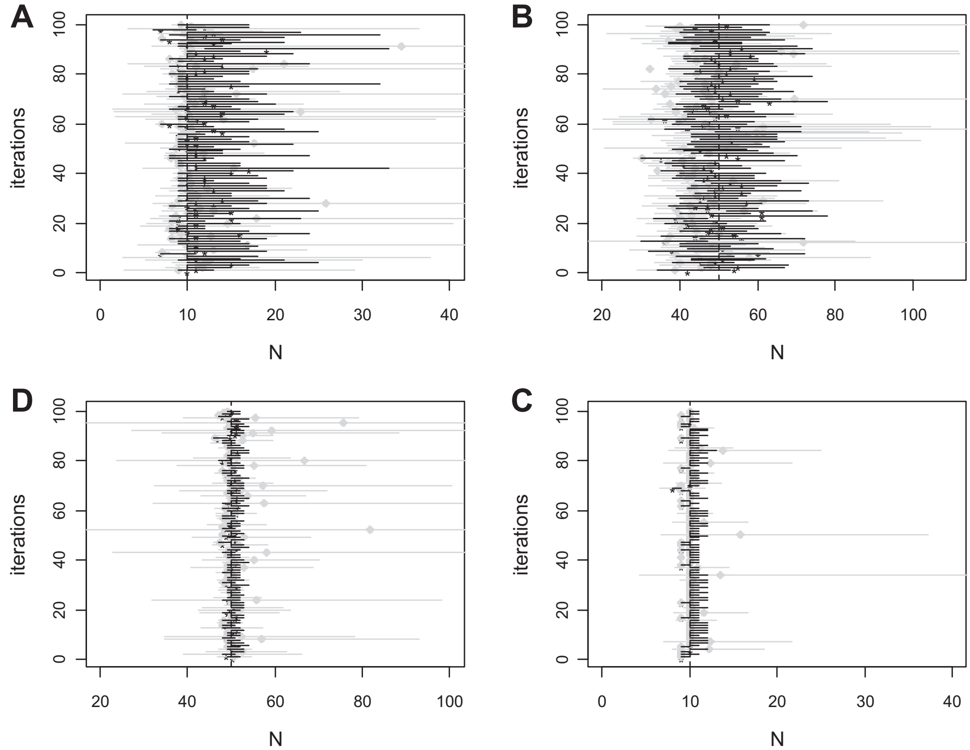

Figure 1. Comparison between abundance estimates obtained from non-spatial models versus spatially explicit capture–recapture (SECR) models according to 4 scenarios mimicking low detection probability and small population size (A), low detection probability and large population size (B), high detection probability and small population size (C) and high detection probability and large population size (D) using simulated data. We provide estimates (dots) and confidence intervals (lines) for the non-spatial model in gray. We display posterior medians (asterisks) and 95% credible intervals (lines) for the SECR model in black. The vertical dashed line indicates the actual value of abundance.

(σ) was estimated to be 1.45 (95% CI: 0.16–0.58). The abundance was estimated to be 12.04 individuals (95% CI: 9.0–18.0). We found extensive spatial variation in the location of estimated activity centers (Fig. 2), most of them being concentrated in the center and in both southeastern and western corners of the trap array.

DISCUSSION

Information on wildlife population responses and dynamics are essential complements to information about human dimensions, habitat, and ecosystem functioning that go into conservation planning and monitoring (Mills 2007). Using the Eurasian lynx as a case study, we demonstrated how cutting-edge analytical methods could be used to

Table 1. Summary of the statistical performance of the non-spatial and spatially explicit capture–recapture (SECR) models using simulated data rising from 4 scenarios mimicking low detection probability (A, B) versus high detection probability (C, D) and small population size (A, C) versus large population size (B, D). We present the root mean square error (RMSE) and either the 95% confidence (non-spatial model) or the 95% credible (SECR model) interval (CI coverage).

Scenario	Relative bias	RMSE	CI coverage (%)
Non-spatial model			
A	0.10	4.00	75
B	−0.08	9.38	76
C	0.01	1.03	78
D	0.03	5.08	73
SECR model			
A	0.12	2.39	97
B	−0.02	5.49	92
C	−0.02	0.47	99
D	0.00	0.89	96

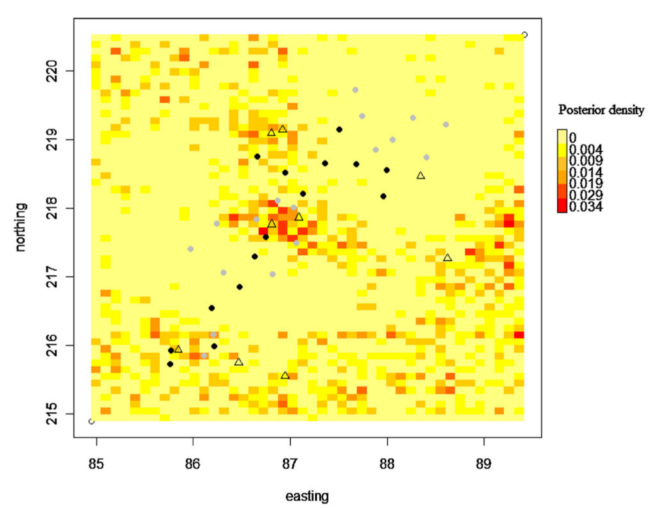

Figure 2. Map of posterior density of lynx activity centers in French Jura department in 2011. Specifically, the map shows E[$N(i)$ | data], where $N(i)$ is the number of activity centers located in pixel i. Colors code for the estimated number of activity centers in each 500 m × 500 m pixel. Triangles indicate mean activity center location for identified individuals, dots indicate camera trap locations, black symbols indicate locations where lynx were photographed, and gray symbols are trap locations where no lynx was captured.

estimate and infer abundance of a rare and elusive species using sound monitoring protocols. Characterizing the status of a population in this way can be an important first step of implementing a conservation strategy.

Although the difference in the relative bias between the non-spatial and the SECR model was trivial, the RMSE and the interval coverage both support the conclusion that the SECR model provided better estimates of abundance. Our simulations highlighted that for scenario A, mimicking the lynx dataset, and scenario C, abundance estimates should be used with caution since the spatial model tended to overestimate the actual abundance; whereas the non-spatial model appeared to be closer to the real abundance value. The positive relative bias may be caused by the proportion of individuals that move out or partially out of the trapping array creating an inflated estimate of abundance. Nevertheless, confidence and credible interval coverage and RMSE revealed that the SECR model performed best for all scenarios. For the scenarios B and D, representing a large population with respectively a low and high detection probability, abundance estimates were closer to the actual value when using the spatial model. The 3 deviation indices (relative bias, RMSE, and interval coverage) supported this conclusion.

Spatially explicit CR modeling is an emerging analytical tool that has mainly been used to estimate densities because it does not rely on the assumption of geographic closure (Efford 2004). Obbard et al. (2010) and Gray and Prum (2012) evaluated the performance of the SECR models while estimating density by comparing density estimates using SECR with those obtained from conventional approach in which the effective survey area was estimated using a boundary strip width. The SECR models were recommended in both studies but they could not infer bias since the actual density was unknown. Efford (2004) and Borchers and Efford (2008) assessed the performance of SECR by simulating data from a regular grid of trap. They used alternative methods for fitting the spatial detection model, that is inverse prediction and maximum likelihood, whereas the current study used data augmentation and MCMC (Royle and Young 2008; Royle et al. 2009*a*, *b*). Regardless of the method, the importance of the spatial nature of the sampling process in capture probability modeling is clearly supported by our findings. Modeling the capture probability also avoids substantial bias in estimating abundance. By making capture probability a function of both the location of the activity centers and their distance from the camera traps, SECR models allow efficient use of spatial information contained in CR data.

We acknowledge that we could not cover all possible scenarios in our simulations. In particular, our results were obtained for scenarios that did not account for specificities of the species biology, such as sex-related differences in home range size (Sollmann et al. 2011). Furthermore, we did not take into account the importance of trap configuration, which can have large effects on the number of individuals detected. In our study, the traps were placed mainly on trails because lynx use the easiest route from 1 location to another. Further work is needed to determine the optimal number and location of traps to optimize the human and financial costs of fieldwork while maximizing the precision of abundance estimates. Simulation studies like the one we have conducted may help in that purpose. Using SECR models allows the incorporation of variables affecting detection probability, hence providing managers the opportunity to modify cameras distribution to improve capture success (Royle et al. 2011).

Non-invasive sampling methods such as camera trapping or molecular tracking are commonly used to monitor elusive and wide-ranging populations of large carnivores, as neither of them requires physical captures. These methods can provide estimates of population parameters, like population size, dispersal distance, population growth rate (Marescot et al. 2011), survival (Cubaynes et al. 2010), recruitment, and immigration rate (Karanth et al. 2006). They are particularly relevant for the Eurasian lynx whose individual coat patterns allow the identification via photographs that can be used with capture–recapture models to estimate abundance and density. Furthermore, camera-trapping only requires a single sampling session, in other words repeated sampling is not required (Efford et al. 2009*a*). However, this technique requires reliable photographs from which individuals can be unequivocally identified, otherwise risking bias in population size estimates (overestimation if 2 photographs belonging to the same individual are considered as 2 different individuals, underestimation if 2 photographs of different individuals are wrongly considered as a single individual). The issue of misidentification error has recently received interest (Yoshizaki et al. 2009, Morrison et al. 2011).

MANAGEMENT IMPLICATIONS

With rare and elusive species, we recommend caution when using standard or even spatially explicit capture–recapture models because few data are available commonly. Even though previous studies have demonstrated the utility of non-invasive sampling methods (e.g., Petit and Valiere 2006) and the analysis of data collected through CR techniques (e.g., Rees et al. 2011) when few data are available, the confidence and credible intervals still remain large. A preliminary simulation study is useful to determine which factors affect abundance estimates (no. of camera traps and their location in particular). To help in this objective, we provide R code to reproduce our simulation exercise and adapt it for one's own purpose (see supplemental information available online at www.onlinelibrary.wiley.com). Pending these precautions, spatially explicit CR models provide useful information that can be used to produce sound management strategies for carnivores. In particular, the density map of the posterior locations of activity centers could be compared to livestock attack distribution maps to determine whether correlations exist between hotspots of attacks on livestock and pools of lynx centers of activity. This might help to predict potential conflicts between human activities and predators.

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