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1 **ABUNDANCE OF RARE AND ELUSIVE SPECIES: EMPIRICAL INVESTIGATION OF CLOSED VS.**
2 **SPATIALLY EXPLICIT CAPTURE-RECAPTURE MODELS WITH LYNX AS A CASE STUDY**

3

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9

10 **ABSTRACT**

11 Effective conservation and management require reliable monitoring methods and estimates of
12 abundance to prioritize human and financial investments. Camera trapping is a non-invasive
13 sampling method allowing the use of capture-recapture (CR) model to estimate abundance
14 while accounting for the difficulty of detecting individuals in the wild. Here, we investigated
15 the relative performance of classical closed CR models and spatially explicit CR models
16 (SECR) that incorporate spatial information in the data. Using simulations, we considered
17 four scenarios comparing low vs. high detection probability and small vs. large populations
18 and confronted abundance estimates obtained from both approaches. Standard and SECR
19 models both provided lowly biased abundance estimates but precision was improved when
20 using SECR models. The associated confidence intervals also provided better coverage than
21 their non-spatial counterpart. SECR models exhibit better statistical performance than
22 standard closed CR models and allow producing sound management strategies through
23 density maps of activity centers. To illustrate the comparison, we considered the Eurasian

24 lynx (*Lynx lynx*) as a case study and provided the first abundance estimates of a local
25 population in France.

26 *Keywords:* abundance, relative bias, camera trapping, capture-recapture models, *Lynx lynx*,
27 root mean square error, simulations, spatially explicit capture-recapture models.

28

29 INTRODUCTION

30 The presence of large carnivores - wolves, bears, lynxes, and wolverines - usually results in
31 strong socio-cultural issues in all societies, Europe making no exception. These species share
32 common features such as large territories and the need for a large mosaic of natural habitat
33 and preys, potentially competing with human activities, e.g., hunting and livestock farming.
34 Such conflicts, in combination with habitat loss, have led to local extinction of large
35 carnivores in many areas. While almost extinct at the beginning of the 20th century in many
36 European countries, large carnivores have slowly recovered via reintroduction or natural re-
37 colonization through dispersal.

38 In this context, the Bern convention (1979), the European Habitats Directive (1992) as well as
39 the International Union for Conservation of Nature (IUCN) Red list provided specific indexes
40 and rules to assess the conservation status of species and to help checking how management
41 decisions could meet the conservation requirements. Abundance was defined as one of the
42 key estimates needed in assessing species' status and is the state variable of interest in most
43 ecological research and monitoring programs involving management and conservation of
44 animal populations (Nichols and MacKenzie 2004). Indeed, reliable estimates of population
45 size are essential to evaluate conservation and wildlife management programs such as
46 reintroduction programs. However, large carnivores are difficult to monitor since they are

47 elusive, living at low densities over wide areas and usually solitary and mostly nocturnal.
48 Exhaustive counts are therefore often expensive, time consuming and sometimes impractical.

49 In order to assess population trends in elusive and wide-ranging population, non-invasive
50 survey methods have been increasingly used over the last decade. In particular, camera-
51 trapping methods combined with capture-recapture (CR) modeling have become a standard
52 tool to estimate carnivores' abundance while accounting for detectability less than 1 (e.g.,
53 tigers *Panthera tigris*: Karanth et al. 2006, Karanth and Nichols 1998; ocelots *Felis pardalis*:
54 Trolle and Kéry 2003; snow leopards *Uncia uncia*: Jackson et al. 2006; jaguars *Panthera*
55 *onca*: Silver et al. 2004). Standard CR models usually assume geographical closure (no
56 movement in or off the sampling grid). However, this assumption is often violated, especially
57 for mammals with large home range. Another major assumption of these models is that no
58 individual within the sampled area has a zero probability of being captured. To deal with these
59 issues, an alternative approach known as spatially-explicit CR modeling (SECR) was recently
60 developed (Royle and Young 2008, Borchers and Efford 2008). This method has been applied
61 to a large number of taxa (e.g., birds: Efford 2004, Borchers and Efford 2008, Efford et al.
62 2009a; cetaceans: Marques et al. 2010; stoats: Efford et al. 2009b; bears: Obbard et al. 2010
63 and lizards: Royle and Young 2008). Here, the probability of detection for each trap is
64 modeled as a function of distance between a latent variable, the individual activity center
65 (equivalent to the home range center), from which animals move randomly, and the camera
66 trap where they have been captured. This model does not rely on the assumption of
67 geographic closure by accounting for the fact that animals move and that detection probability
68 depends on their center of activity (Gardner et al. 2009).

69 In this paper, our objectives were twofold. First, we aimed at evaluating the relative
70 performance of SECR methods vs. conventional non-spatial CR models in estimating

71 abundance in the context of carnivore conservation. Most of the studies assessing bias in
72 spatial models compared abundance estimates using real datasets rather than simulated data,
73 hence the impossibility to infer bias and precision (e.g., Gardner et al. 2009). Recent papers
74 dealing with SECR models and simulations (Efford 2004, Royle and Young 2008, Borchers
75 and Efford 2008, Efford 2011) focused on the performance of different methods to estimate
76 density (e.g., nested subgrid vs. inverse prediction, likelihood-based vs. Bayesian methods)
77 but did not formally compare SECR and non-spatial models. Therefore, we carried out a
78 simulation study with several scenarios comparing low vs. high detection probability and
79 small vs. large populations to quantify the performances of parameter estimates using both
80 SECR and non-spatial models. We also suggested how the simulations results could be used
81 to improve the trapping design when necessary. Second, we used the two methods to analyze
82 a real dataset from a camera-trapping experiment with the Eurasian lynx (*Lynx lynx*) in the
83 French Jura Mountains. This population originates from reintroductions in Switzerland in the
84 70's. Although listed as a species of Least Concern given its wide range (IUCN, 2001), habitat
85 loss, prey depletion, and poaching are still regarded as potential threats. Up to now, the main
86 monitoring program for lynx in France was based on indirect signs (i.e., tracks, scat, hair, and
87 other signs) collected by a network of volunteers (state employees, hunters, naturalists,
88 farmers, and mountain guides). While the use of indirect signs is often the most effective and
89 least expensive method for estimating the distribution of carnivores, the resulting estimates of
90 population parameters such as abundance are often approximate. Camera-trapping monitoring
91 has recently been initiated in France in order to monitor lynx population and evaluate the
92 conservation status of a population where problematic interactions between hunters and lynx
93 exist. We provided the first estimate of Lynx abundance for this French population. Finally,
94 recommendations are provided for the conservation of elusive species, with an emphasis on
95 large carnivores and their monitoring.

96 MATERIAL AND METHODS

97 Simulation study design

98 We considered that our population was demographically and geographically closed (i.e. no
99 birth, death, immigration or emigration during the sampling period) to apply CR models to
100 estimate abundance. Lynx are long-lived animals (Sunquist and Sunquist 2002) and the
101 camera-trap sampling period was made short enough so that no deaths or births were assumed
102 to occur during this period. In addition, the trapping session was timed outside the dispersal
103 period for subadults.

104 In order to compare the performance of the standard vs. the SECR methods in estimating
105 abundance, we simulated 100 datasets with a particular spatial organization. We considered
106 four scenarios comparing low vs. high detection probability and small vs. large populations.
107 These scenarios were used to evaluate relative bias in parameter estimates, the precision and
108 the coverage of 95% confidence and credible intervals (CI hereafter for Bayesian credible
109 intervals or Frequentist confidence intervals indistinctively). Each dataset was created using
110 the traps configuration from the monitoring of the lynx in the study area (see case study
111 below) but we did not use any constraints to mimic lynx behavior simulating the datasets. The
112 number of capture occasions was set to $k = 15$ and the actual population size to $N = 10$ or $N =$
113 50 depending on the scenario. The simulations were based on the SECR model formulation.
114 We simulated N individual activity centers using their coordinates. Then, we evaluated
115 whether we could *a posteriori* reliably estimate from the model the actual number and
116 location of activity centers we had simulated. We proceeded to the simulation in two steps,
117 first a point process component that describes the spatial distribution of the centers of activity,
118 second an observation process component that makes the connection between the detection of
119 an individual and its center of activity given the spatial distribution of traps.

120 *a) Point process*

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

$$125 \quad s_i \sim \text{Uniform}(S) \quad (\text{Eq. 1})$$

126 In order to simulate capture histories we assumed that the probability of each individual to be
 127 captured was a function of the distance between its activity center and the trap.

128 *b) Exposure to traps*

129 The detection probability of an individual at a given trap was a decreasing function of the
 130 distance from the activity center to that trap: the further the activity center was from the trap,
 131 the less likely the animal was exposed to capture. Thus, we first defined a distance matrix $D_{i,j}$
 132 as the Euclidean distance between every activity centers i and trap j :

$$133 \quad D_{i,j} = \sqrt{(s_{xi} - x_j)^2 + (s_{yi} - y_j)^2} \quad (\text{Eq. 2})$$

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

$$136 \quad E0_{i,j} = \lambda_0 \exp\left(-D_{i,j}^2 / \sigma\right) \quad (\text{Eq. 3})$$

137 where λ_0 is the baseline encounter rate, i.e. the expected number of captures of individual i at
 138 trap j during a sampling occasion when an individual's activity center s_i is located precisely at
 139 trap j , and parameter σ (in km) controls the shape of the distance function, reflecting how fast

140 the exposure decreases with distance. The greater σ is, the faster the exposure decreases with
141 distance.

142 *c) Capture process*

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

$$147 \quad p_{i,j} = 1 - \exp(-E_{i,j}) \quad (\text{Eq. 4})$$

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

160 **Model formulation**

161 *a) Standard CR models*

162 We first calculated abundance estimates by accounting for detection probabilities using
163 standard CR models. We considered different sources of variation in capture probabilities. In
164 addition to a model with no variation in the detection probability (model M_0), we considered
165 behavioral responses to trapping (model M_b), differences in capture probabilities over time
166 (model M_t), while the most complex models included among-individual heterogeneity in
167 capture probabilities (model M_h) (Otis et al. 1978, Williams et al. 2002). In addition, we
168 considered four models that were combinations of these sources of variation (Models M_{bh} ,
169 M_{th} , M_{tb} , and M_{tth}). For each simulated dataset, the Akaike's Information Criterion (AIC) was
170 used to select the model that best described our dataset (Burnham and Anderson 2002). These
171 analyses were achieved via maximum likelihood with the R package Rcapture (Baillargeon
172 and Rivest 2007).

173 *b) SECR model implementation using a Bayesian approach*

174 Each camera trap reflected the location of capture, which, in turn, provided insight into the
175 activity centers coordinates of each lynx. The SECR model has the advantage to incorporate
176 spatial heterogeneity while estimating abundance (Royle et al. 2009a, Royle et al. 2011, Royle
177 et al. 2009b). More specifically, the SECR model makes explicit the distinction between a) a
178 latent component for the spatial point process of the (unknown) location of the activity centers
179 (Eq. 1) and b) an observation component that describes how the observed data arise from the
180 point process (Eq. 4).

181 We adopted a Bayesian approach (McCarthy 2007) to fit the SECR model. It made the
182 analysis convenient as the activity centers are treated as random effects that are relatively easy
183 to deal with in the Bayesian framework (King et al. 2009). The Bayesian approach combines
184 the likelihood with prior probability distributions of the parameters to obtain the posterior
185 distribution of the parameters of interest based on Bayes' theorem. We used Markov Chain

186 Monte Carlo (MCMC) methods to simulate observations from the posterior distributions.
187 Regarding priors for parameters, we considered that we did not have any information about
188 the spatial distribution of the activity centers of the simulated individuals thus we assumed
189 they were uniformly distributed over S. We chose a Uniform(0,15) distribution for σ and we
190 assigned a Gamma(0.1,0.1) distribution to λ_0 .

191 To obtain an estimate of abundance, we used a data augmentation approach (Royle and Young
192 2008). We augmented the data set with 100 individuals and we associated to every individual
193 a latent indicator z_i . The encounter histories of the 100 individuals initially contained only
194 zeroes. Some of these individuals were not captured during the intensive camera trapping but
195 belonged to the population. The z_i indicator reflects the probability ψ of an individual to be a
196 member of the population. We assumed a Uniform(0,1) prior for ψ that we added as an
197 additional layer to our model. We defined z_i as a binary variable equals to 0 when the
198 individual i is not a member of the population and 1 otherwise.

199 The abundance N was obtained as a derived parameter by adding all the presence indicators
200 z_i . These analyses were implemented in WinBUGS (Spiegelhalter et al. 2003) called from R
201 using package R2WinBUGS (Sturtz et al. 2005).

202 *c) Evaluating the performance of the two methods*

203 We evaluated the performance of the standard CR models and the SECR models by
204 comparing the abundance estimates of the two methods used on each 100 datasets simulated
205 to the true value of abundance. As a result, we were able to quantify the potential bias in
206 parameter estimates obtained for both models. We looked at the relative bias in \hat{N} , the
207 estimator of N, calculated as $(E[\hat{N}] - N) / N$ which can be approximated as the average over
208 the 100 iterations of the difference between the estimated abundance under the model

209 considered and the true parameter value $\hat{a}_{i=1}^{100} \hat{N}_i / 100 - N$. To assess the precision, we
210 calculated the Root Mean Square Error (RMSE) as $\sqrt{E(([\hat{N}] - N)^2)} \gg \sqrt{\hat{a}_{i=1}^{100} (\hat{N}_i - N)^2 / 100}$.
211 A low RMSE is characteristic of a good trade-off between low bias and high variance. Finally,
212 we looked at the 95% confidence interval coverage by determining and averaging over all
213 simulations whether the interval contained the true value.

214 **Eurasian lynx in French Jura Mountains**

215 Lynx is a solitary nocturnal species, living in forested areas. It can be individually identified
216 based on the photographs of their unique pelage patterns (e.g., Zimmermann and
217 Breitenmoser 2007). Our study area was located in the French department of Jura. A 480 km²
218 zone was considered in the southern center of the Jura department between the Vouglans lake
219 and the southern border of Doubs department. This study area was delimited using knowledge
220 on lynx habitat and forest continuity. In order to maximize detectability, several steps were
221 followed: 1) Camera traps were set at optimal locations (on game path, hiking trail, forest
222 road) based on previous signs of lynx presence and on local knowledge; 2) In theory, all
223 individuals should have a non-null detection probability to use standard capture-recapture
224 models (Karanth and Nichols 1998). It is not necessary for SECR models (Royle et al. 2009a).
225 Thus, the study area was divided into a grid of 2.7 km × 2.7 km cells (Zimmermann et al.
226 2007) where one of two cells was sampled, leading to 33 cells sampled from February to
227 April 2011. This grid size and sampling design ensure that at least one camera trap site is set
228 in each potential lynx home range; 3) At each trapping site, two camera traps with infrared
229 trigger mechanism were set in order to photograph both flanks of the animal allowing a high
230 level of confidence in individual identification. Date, time and location of each photographic
231 capture of a lynx were recorded; 4) Camera traps were checked weekly to change memory

232 cards and batteries. The sampling period was divided into 15 occasions, one occasion being
233 defined as 4 successive trap nights. The results of the SECR model were used to build a
234 density map of the lynx activity centers. For each of the MCMC iterations, we plotted the
235 centers of activity of the individuals belonging to the population ($z_i = 1$) on successive layers.
236 For every layer, we divided the region S into squares of 500×500 m then we calculated the
237 mean number of activity centers falling into each square. R and WinBUGS codes are
238 available on request from the first author.

239 **RESULTS**

240 **Simulation study to compare spatial vs. non-spatial models**

241 For each scenario and each simulated dataset, we reported the abundance posterior median
242 estimate and its 95% credible interval for the SECR model and the abundance point estimate
243 with its 95% confidence interval from the non-spatial model (Fig. 1). Scenario A represented a
244 small population with a low detection probability mimicking the Eurasian lynx dataset. Both
245 models similarly slightly overestimated abundance: the non-spatial model displayed a relative
246 bias of 0.096 and the SECR model relative bias was 0.121. Scenario B represented a large
247 population with a low detection probability. The non-spatial model clearly underestimated the
248 population size with a relative bias of -0.08 while the SECR model slightly underestimated it
249 with a -0.016 relative bias. Scenario C corresponded to a small population with a high
250 detection probability. For most datasets, the non-spatial model provided estimates close to the
251 actual abundance (relative bias around 0.007) but with large confidence intervals and the
252 SECR model also provided unbiased estimates (relative bias around -0.02) and small credible
253 intervals. Finally, scenario D represented an ideal situation with a large population and a high
254 detection probability. The non-spatial model slightly overestimated abundance (relative bias =
255 0.026) while the SECR model provided values close to the actual abundance (relative bias =

256 0.0002). RMSE clearly revealed that the SECR model provided a better balance between bias
257 and variance for all scenarios than the non-spatial model. With regard to CI coverage, the
258 confidence interval of the non-spatial model included the true abundance value in only 73 to
259 78 out of the 100 simulated datasets depending on the scenario. The credible interval of the
260 SECR model included the true value in 92 to 99 datasets (Table 1). Credible intervals of the
261 SECR model provided better coverage than confidence intervals as provided by standard
262 closed CR models.

263 **Lynx case study**

264 Data were collected between February and April 2011 from 33 trap sites resulting in 1980 trap
265 nights. One site was found effective during less than 50% of the trapping nights. It was
266 removed from the analysis reducing the theoretical effort to 1816 effective trapping nights.
267 The study provided an encounter history for 9 individuals that were photographed on 14 of
268 the 32 trap sites. Individuals were captured on up to six different sites and the maximum
269 distance moved by one individual between captures was 27.6 km. Model selection ranked M_h
270 incorporating individual heterogeneity in capture probability as the best model followed by
271 M_0 assuming constant capture probability. Average estimated detection (over individuals) was
272 0.14 and the estimated abundance using M_h was 12 individuals (95% CI 7.14–20.27). For the
273 SECR model, the baseline encounter rate at a given camera (λ_0) was 0.05 photographs
274 occasion⁻¹ (95% CI 0.03–0.15) while the movement parameter σ was estimated to 1.45 (95%
275 CI 0.16–0.58). The abundance was estimated to 12.04 individuals (95% CI 9.0–18.0).
276 Posterior estimates of activity centers' locations of the 9 individuals photographed are shown
277 in Fig. 2. There was a lot of spatial variation in the location of estimated activity centers, most
278 of them being concentrated in the center and in both south-eastern and western corners of the
279 trap array.

280 DISCUSSION

281 Information on wildlife population responses and dynamics are essential complements to the
282 human dimensions, habitat, and ecosystem functioning that go into conservation planning and
283 monitoring (Mills 2007). Using the Eurasian lynx as a case study, we demonstrated how
284 cutting-edge analytical methods could be used to estimate and infer abundance of a rare and
285 elusive species using sound monitoring protocols. This is a crucial step when implementing
286 any conservation strategy so as to be able e.g. to characterize the population status before any
287 action is undertaken, and re-evaluate it once management has been engaged.

288 Comparison of abundance estimates from spatial vs. non-spatial models

289 Albeit the difference in the relative bias between the non-spatial and the SECR model is
290 trivial, the RMSE and the CI coverage both support the conclusion that the SECR model
291 provides better estimates of abundance. Indeed, our simulations have highlighted that for
292 scenario A, mimicking the lynx dataset, and scenario C, abundance estimates should be used
293 with caution since the spatial model tended to overestimate the actual abundance while the
294 non-spatial model appeared to be closer to the real abundance value. The positive relative bias
295 may be caused by the proportion of individuals that move out or partially out of the trapping
296 array creating an inflated estimate of abundance. Nevertheless, confidence and credible
297 interval coverage and RMSE revealed that the SECR model performed best whatever the
298 scenario we considered. For the other scenarios, B and D - representing a large population
299 with respectively a low and high detection probability - abundance estimates were closer to
300 the actual value when using the spatial model. The three deviation indices (relative bias,
301 RMSE and interval coverage) supported this conclusion.

302 Spatially-explicit CR modeling is an emerging analytical tool that has mainly been used to
303 estimate densities because it does not rely on the assumption of geographic closure (Efford
304 2004). Obbard et al. (2010) and Gray and Prum (2012) evaluated the performance of the
305 SECR models while estimating density by comparing density estimates using SECR with
306 those obtained from conventional approach in which the effective survey area is estimated
307 using a boundary strip width. SECR models were recommended in both studies but they could
308 not infer bias since the actual density was unknown. Efford (2004) and Borchers and Efford
309 (2008) assessed the performance of SECR by simulating data from a regular grid of trap.
310 They used alternative methods for fitting the spatial detection model, that is inverse prediction
311 and maximum likelihood while the current study used data augmentation and MCMC (Royle
312 and Young 2008; Royle et al. 2009a, b). Regardless of the method, the importance of spatial
313 nature of the sampling process in capture probability modeling is clearly supported by our
314 findings. Modeling the capture probability also avoids substantial bias in estimating
315 abundance. By making capture probability a function of both the location of the activity
316 centers and their distance from the camera traps, SECR models allow efficient use of spatial
317 information contained in CR data.

318 We acknowledge that we could not cover all possible scenarios in our simulations. In
319 particular, our results were obtained for scenarios that did not account for specificities of the
320 species biology, such as sex-related differences in home range size for instance (Sollmann et
321 al. 2011). Furthermore, we did not take into account the importance of traps configuration that
322 can have large effects on the number of individuals detected. In our study, the traps were
323 placed mainly on trails because lynx use the easiest way to go from one location to another.
324 Further work is needed to determine the optimal number and location of traps in order to
325 minimize the human and financial costs of fieldwork while maximizing the precision of

326 abundance estimates. Simulation studies like the one we have conducted here may help in that
327 purpose. SECR models allow the incorporation of variables affecting detection probability
328 hence providing managers the opportunity to modify cameras distribution to improve capture
329 success (Royle et al. 2011).

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

345 **Management implications**

346 With rare and elusive species, we recommend caution when using standard or even spatially-
347 explicit capture-recapture models since commonly few data are available. Even though
348 previous studies have demonstrated the utility of non-invasive sampling methods (e.g., Petit
349 and Valière 2006) and the analysis of data collected through CR techniques (e.g., Rees et al.

350 2011) when few data are available, the confidence and credible intervals still remain large. A
351 preliminary simulation study is useful to determine which factors affect abundance estimates
352 (number of camera traps and their location in particular). To help in this objective, we provide
353 R code to reproduce our simulation exercise and adapt it for one's own purpose (See
354 Supplementary Information). Pending these precautions, spatially explicit CR models provide
355 useful information that can be used to produce sound management strategies for carnivores. In
356 particular, the density map of the posterior locations of activity centers could be confronted to
357 livestock attacks distribution maps to determine whether correlations exist between hotspots
358 of attacks on livestock and pools of lynx centers of activity. This might help to predict
359 potential conflicts between human activities and predators.

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365 camera-trapping session.

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462

463 **CAPTIONS**

464

- 465 Table 1. Summary of the statistical performance of the non-spatial and SECR models. The
466 RMSE is the Root Mean Square Error and CI is either the 95% confidence (non-spatial
467 model) or the 95% credible (SECR model) interval.

| | 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% |

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470 Fig. 1. Comparison between abundance estimates obtained from non-spatial models vs. SECR
 471 models according to four scenarios (low detection probability (A,B) vs. high detection
 472 probability (C, D) and small population size (A,C) vs. large population size (B, D)). With grey
 473 dots and lines we displayed respectively estimates and confidence intervals for the non-spatial
 474 model. With black asterisk and black lines we displayed posterior means and 95% credible
 475 intervals obtained with the SECR model. The vertical dashed line indicates the actual value of
 476 abundance.

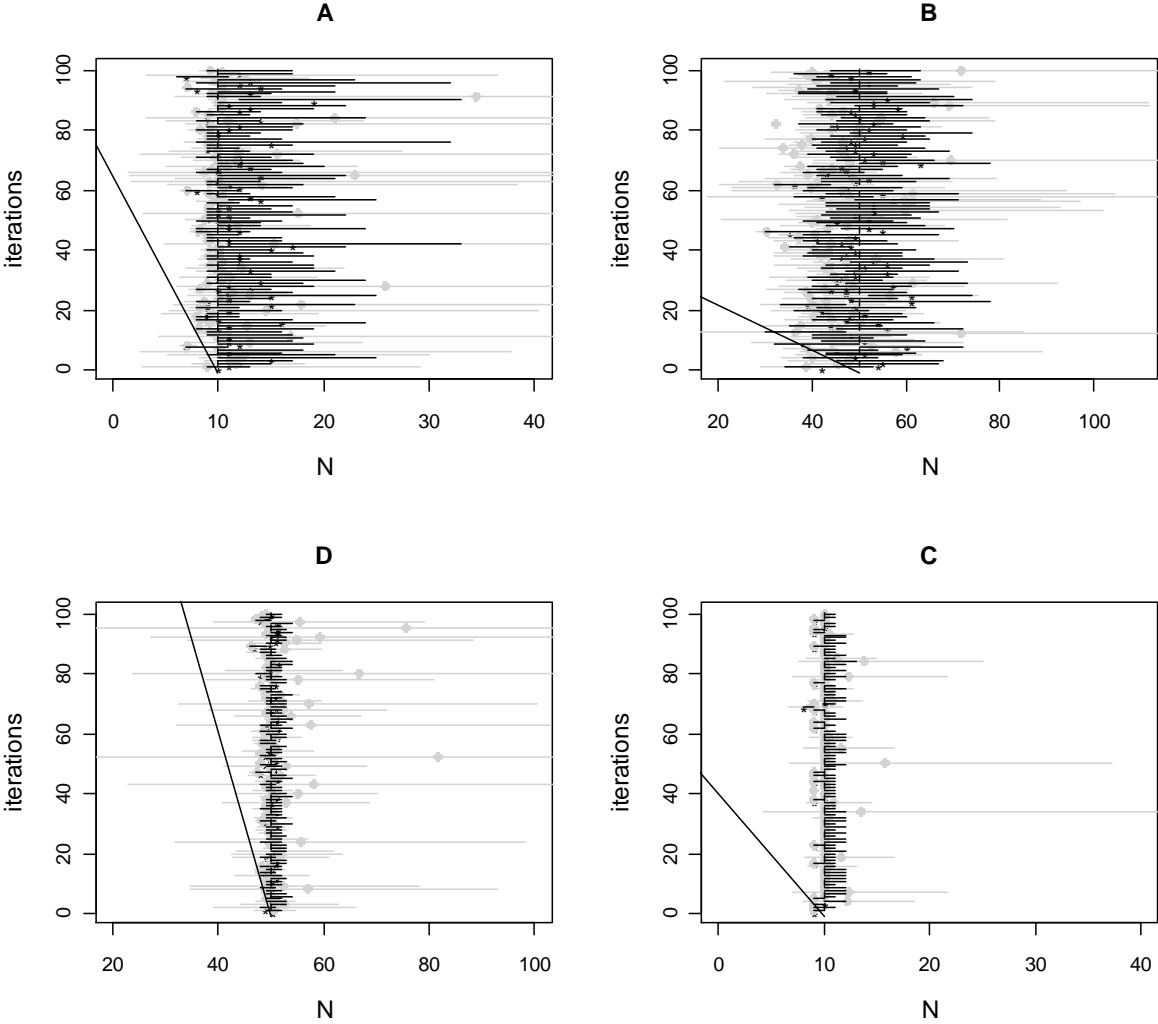
477 Fig. 2. Map of posterior density of lynx activity centers in French Jura department.

478 Specifically, the map shows $E[N(i) | \text{data}]$, where $N(i)$ is the number of activity centers
 479 located in pixel i . Colors code for the estimated number of activity centers in each $500 \times$
 480 500m pixel; triangles indicate mean activity center location for identified individuals; dots
 481 indicate camera trap locations; black ones indicate locations where lynx were photographed
 482 and grey ones where no lynx was captured.

483

484 Fig. 1

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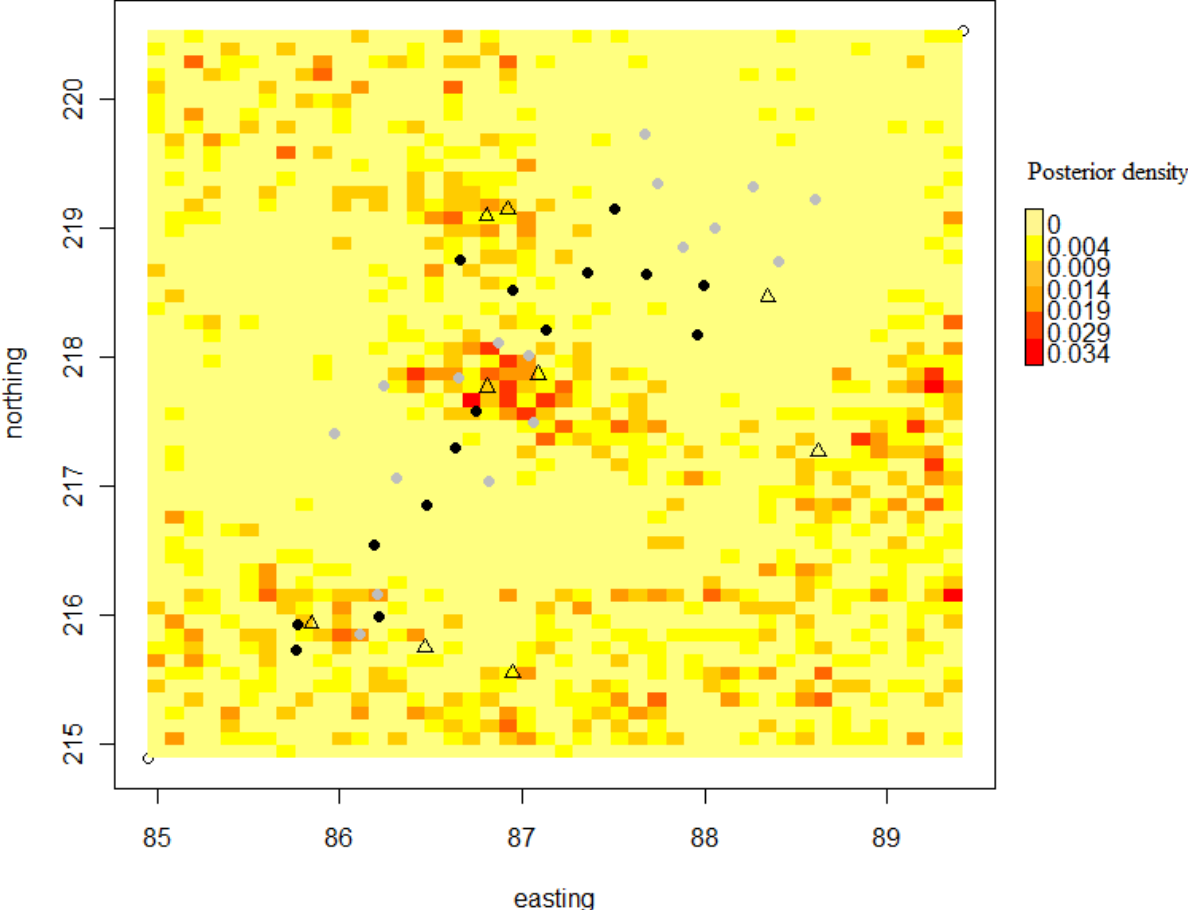


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488 Fig. 2

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