

MASTER 2 « Biodiversity Ecology Evolution » internship report Course: Evolutionary and Behavioral Ecology

Estimating the population size of the Eurasian lynx (*Lynx lynx*) in Croatia using camera-trapping and spatial capture-recapture modelling



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Course of the internship

My internship started on 3rd January 2022 and is expecting to end on 30th of June 2022. No obstacles occurred during my internship. In addition to my main work of computer modelling, I was also participating in camera-trapping management, lynx captures and autopsies.

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Abstract

In 2017, the LIFE Lynx project (LIFE16 NAT/SI/000634) started a reinforcement process in order to save the Dinaric population of the Eurasian lynx (*Lynx lynx*) from extinction. The monitoring of the population demography and dynamics became critical to assess the success of the translocations of lynx which started in 2019. Camera traps proved to be an efficient way to detect the presence of rare and elusive species, such as the lynx. The data collected can be analyzed by spatial capture-recapture (SCR) modelling, an advanced method compared to the traditional non-spatial capture-recapture. This study provides the estimates of the lynx density and abundance in Croatia through the analysis of camera trapping data collected from August 2019 to April 2020 by SCR modelling. The results showed to be in the lower range of the density estimates from other studies on lynx populations in Europe. Though, several factors limit this comparison, including the sampling design and the integration of covariates in modelling. A discussion about the precision of the estimates and potential sources of bias is also provided.

Key words: abundance, density, oSCR, covariates, capture probability, marking sites, home-range size.

Résumé

En 2017, le projet LIFE lynx (LIFE16 NAT/SI/000634) a initié un processus de renforcement de la population dinarique du lynx eurasien (*Lynx lynx*) menacée d'extinction. Le suivi de la démographie et de la dynamique de la population est devenu essentiel pour évaluer le succès des translocations de lynx ayant débuté en 2019. Les pièges photographiques se sont avérés être un moyen efficace pour détecter la présence d'espèces rares et élusives, comme le lynx. Les données recueillies peuvent être analysées par modélisation de capture-recapture spatiale (CRS), une méthode plus avancée que la méthode traditionnelle de capture-recapture non spatiale. Cette étude fournit les estimations de la densité et de l'abondance de lynx en Croatie par l'analyse des données de piégeage par caméra collectées d'août 2019 à avril 2020 par modélisation CRS. Les résultats semblent se situer dans la fourchette inférieure des estimations de densité provenant d'autres études sur les populations de lynx en Europe. Cependant, plusieurs facteurs limitent cette comparaison, notamment le design expérimental et l'intégration de covariables dans la modélisation. La précision des estimations et les sources potentielles de biais sont également discutées.

Mots clés: abondance, densité, *oSCR*, covariables, probabilité de capture, sites de marquage, domaine vital.

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Table of acronyms

95% CI: 95% Confidence Interval CR: capture-recapture dAIC: Akaike Information Criterion differences edf: encounter data file mmdm: mean maximum distance moved SCR: spatial capture-recapture SECR: spatially explicit capture-recapture tdf: trap deployment file

I. Introduction

Among the four species of lynx (genus *Lynx*) that are distributed over most of the Holartic, two of them are present in Europe: the Eurasian lynx (*Lynx lynx*) and the Iberian lynx (*Lynx pardinus*). Only the Eurasian lynx (referred to as lynx below) is present in Croatia and belongs to the Dinaric population, one of the 11 populations that live in Europe. European lynx populations greatly differ by their conservation status, even though lynx is classified as "least concern" by the IUCN Red List (https://www.iucnredlist.org/).

At the beginning of the 20th century, the lynx was extirpated from the Dinaric mountains because of habitat loss, depletion of its prey and human persecution (Kratochvil et al., 1968). Motivated by the desire to restore this game species, the lynx was successfully reintroduced by hunters in 1973 in Slovenia and quickly spread towards the south-east to Croatia and Bosnia and Herzegovina, as well as to Italy in the west and Austria in the north (Sindičić et al., 2013). The favorable habitat and the abundance of prey species contributed to the growth and stabilization of the population until the early 1990s. At the beginning of the 21st century the population started to decrease, mainly due to human-induced mortality, low genetic variability and prey base depletion (Potočnik et al., 2009; Sindičić et al., 2013, 2016). The size of the population was estimated at 130 individuals, with 40 to 60 individuals in Croatia, based on experts estimation but without proper monitoring (von Arx et al., 2004). Since 1998 lynx is classified as a strictly protected species in Croatia (Frković, 2001), while the conservation status of the lynx population was assessed as unfavorable in the Habitat Directive report for the period of 2013-2018 (Kusak et al., 2019). In order to save the population from another extinction, a reinforcement process started in 2017 under the LIFE Lynx project (Preventing the Extinction of the Dinaric-SE Alpine Lynx Population Through Reinforcement and Longterm Conservation; LIFE16 NAT/SI/000634; https://www.lifelynx.eu/). The assessment and monitoring of the population demography and dynamics became critical to apply appropriate management measures for the conservation of the lynx in the long term.

For two decades now, camera trapping has been extensively used to detect the presence of animals in defined areas. This method is considered as the most effective and cost-efficient methodology as it is non-invasive, causes minimal disturbance for wildlife, allows intensive and prolonged data collection over large and remote areas, and provides objective records of an animal's presence. Therefore, it is of particular interest in research of rare and elusive species such as the lynx. Moreover, in the case of the lynx and spotted cats in general, camera trapping allows the identification of individuals through their unique pelage pattern which does not vary in time (Rovero & Zimmermann, 2016). The count of the distinct individuals captured by the camera-traps provides the minimum population size. In 2018, camera trapping was implemented at a wide scale in Croatia and leaded to the first scientifically-based estimation of the minimum lynx population size in the country, which ranged between 69 and 82 individuals for the period of 2019-2020 (Gomerčić et al., 2021).

The distribution of the capture events, i.e., when an individual is photographed by a camera-trap, of one individual over a certain period constitutes an encounter history. The statistical modelling of encounter histories can provide an estimate of the fraction of the population that has not been captured and hence an estimation of the total number of individuals in the population, i.e., the abundance. These models are referred to as capture-recapture (CR) models (Otis et al., 1978; Huggins, 1989; White & Burnham, 1999) and have been used for a large range of species, including the lynx (Zimmermann et al., 2007; Weingarth et al., 2012). While the abundance of a population is site-specific, the density allows for comparison between different study areas or temporal sessions. However, one major limitation of the CR models is that the density is derived from the abundance estimate by dividing it with the effective sampling area. Therefore, density is highly sensitive to the size of this user-defined area. Moreover, the spatial variation in the distance between an animal's activity center and the traps results in individual heterogeneity in capture and can lead to biased demographic estimates. To circumvent these problems, more advanced methods have been developed and integrate both the spatial nature of the sampling and the spatial distribution of individuals. They are defined as spatial capture-recapture models (SCR; also mentioned as spatially explicit CR models or SECR). In these models, the probability of capture for each trap is modelled as a function of the distance between a latent variable, the individual activity center (equivalent to the home range center) from which animals move randomly, and the camera trap location where they have been captured (Borchers & Efford, 2008; Efford et al., 2009; Royle et al., 2014). Several studies compared the performances of parameter estimations with SCR versus non-spatial CR models and demonstrated that the estimates were more reliable with the former (Sollmann et al., 2011; Blanc et al., 2013; Efford & Fewster, 2013; Pesenti & Zimmermann, 2013). Density estimates of lynx populations using SCR models are now available for several regions: Switzerland (Pesenti & Zimmermann, 2013), Turkey (Avgan et al., 2014), France (Gimenez et al., 2019), Slovakia (Kubala et al., 2019), Central Europe (Palmero et al., 2021), and the Western (Dul'a et al., 2021) and Romanian Carpathians (Iosif et al., 2022); allowing for comparison.

While SCR models have been specifically developed for accommodating individual heterogeneity due to their different spatial location and distance to traps, other sources of individual heterogeneity in capture can be accounted for, as in conventional CR models (Sutherland & Royle, 2016), in the form of individual covariates. In particular, the inclusion of the sex as a covariate is recommended for species for which there are great differences between the sexes in their behavior and space use, leading to differences in capture probability and movements (Gardner, Royle, et al., 2010; Sollmann et al., 2011; Royle et al., 2015). The lynx is one of these species with males having larger home range sizes which can overlap with the home ranges of one to three females. Adult males also regularly patrol their territory borders, to deposit scent marks and to defend their territory against potential intruders (Breitenmoser-Würsten et al., 2001; Herfindal et al., 2005). Moreover, during the mating season, i.e., from mid-February to mid-April, males move back and forth between the females living in their territory in order to check for their readiness to mate (Breitenmoser-Würsten et al., 2001), resulting in a higher capture probability. Concerning the females, they use a reduced part of their home range during the birth and lactation seasons, i.e., from May to August, which can result in a lower capture probability during this period, while larger and more frequent movements are reported during the pre-mating and mating seasons, as for males (Zimmermann et al., 2005, 2013). SCR models have the other advantage over CR models to be able to include spatial covariates which are covariates associated with the habitat or the trap locations. For the lynx monitoring, camera-traps are usually set at particular positions that could maximize the capture probability. Marking sites are locations of choice as it has been observed that lynx of both sexes scent-marked with a higher marking activity during the mating season and with males visiting marking sites more often than females (Vogt et al., 2014). Moreover, camera trapping at marking sites can yield high quality records as an animal typically exposes all sides of its body while exhibiting marking behavior (Dul'a et al., 2021). Other suitable sites are along forest roads and trails that are likely to channel lynx movements, especially during winter because of snow height (Zimmermann et al., 2013; Gomerčić et al., 2021).

The aim of this study was to estimate the size, i.e., density and abundance, of the lynx population in Croatia for the period of 2019-2020 using capture-recapture data collected from camera traps and a SCR analysis including the sex of the individuals and the type of traplocation (marking sites, roads or other) as covariates. The results would constitute the pre-reinforcement population size, as the first translocations of lynx under the LIFE Lynx project started in May 2019. The capture probability and spatial scale parameter were expected to be higher for males than for females.

II. Materials and Methods

A. Study area and sampling design

The study area encompassed the regions of Gorski kotar, Lika and Northern Dalmatia in Croatia, delimited by the border with Slovenia in the North and the end of the Velebit mountains in the South. It included the Velebit Nature Park and three National Parks: Plitvice lakes, Northern Velebit and Paklenica. The lynx distribution, based on all available observations of presence (Gomerčić et al., 2021), was estimated at 9,501 km² (Figure 1). As part of the Dinaric karst region, the habitat is composed of rugged karst terrains with altitudes ranging from sea level up to 2,000 meters high. Forest is present on higher parts of the plateaus and mountains, and is gradually composed of pubescent oak, beech, and fir forests. Several types of climates prevail in the area: a Mediterranean climate with dry and hot summers and wet and fresh winters along the Adriatic Sea coast; a moderate continental climate in intermountain basins; and a mountainous climate on higher elevations. The average precipitation is about 800 mm per year (Zupan Hajna, 2019). Snowfalls can occur from December to April.

An extensive network of camera traps (Figure 1) was used over the core area of lynx distribution that was divided into 10 x 10 km Pan-European grid (EEA Reference Grid -European Environment Agency, 2017). At least one non-baited camera trap was systematically placed within each 10 x 10 km grid cell, resulting in a total of 88 camera traps set for the study. Different brands and models of camera traps were used, all with active infrared sensor and infrared flash, set to capture one picture and 30 seconds of video or three pictures without the video. To maximize lynx detectability camera traps were set at optimal locations within cells, where landscape and terrain features were likely to channel lynx movements, i.e., lynx marking site, forest roads or wildlife paths. Marking sites were usually abandoned houses or prominent objects, such as tree trunks, and they were always associated with signs of presence (e.g., direct observations, footprints, hair). In some areas, surveillance was limited due to land mines and high disturbance due to logging activities. Therefore, camera trapping was adjusted over space and time to certain areas that were believed to be potentially best for lynx detection and where it was safe to conduct fieldwork. Camera traps were checked approximately every two months when the responsible person replaced the batteries, collected the data from SD card and noted their activity that was important to define trap operability for each of them. The maintenance of camera traps benefitted from the collaboration with local rangers, foresters, and hunters.



Figure 1: Camera trapping survey area of the lynx in Croatia.

Locations of camera traps within the lynx distribution area, according to their type. Camera traps which successfully captured one lynx or more during the study are emphasized.

When managing the camera trap data a capture event was defined as one animal captured over 10 minutes, i.e., if several photographs of the same individual were taken within 10 minutes, only one event was counted. The time frame of the data analyzed started from 15th August 2019 to 15th April 2020 (i.e., 244 days). Therefore, the potential sampling effort, defined as the number of camera traps used multiplied by the number of days they were in operation, was 21,472 trap-days.

B. Lynx identification

A preliminary sorting removed all the empty photographs and videos, i.e., images with no animal presence. Photographs of all lynx capture events were archived in the Faculty of Veterinary Medicine of Zagreb database (Gomerčić, 2017) which is publicly available (http://lynx.vef.hr). Photographs of other species were stored in a different database for other studies (Camelot; Hendry & Mann, 2017). Lynx identification and data processing followed minimal camera trapping reporting standards defined by Choo et al. (2020). Individuals were identified by comparing the pictures taken by the camera traps with a database of reference pictures of already known individuals from previous live-captures and camera trap studies (Erreur ! Source du renvoi introuvable.). The flank side from which the identification was made was specified, i.e., either left or right side only, or both; as the fur pattern of one side can differ from the other side on the same individual. This specification leads to the definition of a minimum and a maximum number of identified individuals, the minimum being the parameter of interest in this study. For example, if the number of individuals identified by their left side only is inferior to the number of individuals identified by their right side only, then the minimum total number would include individuals identified by both sides and the ones identified by their right side only. Another characteristic considered in the identification process was that only independent adult or subadult individuals were included in the study, i.e., juveniles captured with their mother were excluded. The sex was also determined when the genital area was clearly visible or when females were seen with their cubs. At least two different observers were involved in the identification process in order to reduce misidentification errors. The observers worked independently. A double check of the photographs was performed by the most experienced observer in case of doubts for one individual. The unidentifiable photographs, e.g., fur pattern not visible or too obscure for reliable identification, were excluded from the study. The videos were not stored in the database but used as additional help for the identification process.



Photographs of the right (A) and left (B) sides of the lynx called *Spot* and captured at different occasions. The method used for the identification was by selecting one particular pattern, usually located on the flank (red line marks) and progressively identified other particular patterns around (blue line marks). This example also illustrates the fact that one individual does not have the same pattern on its two sides (Rovero & Zimmermann, 2016).

C. SCR analysis

The SCR analysis in this study was performed using the *oSCR* package in R implemented in a maximum likelihood estimates framework (Sutherland et al., 2019; R Core Team, 2021).

1. General description

SCR models assume that a population of N individuals is sampled, and that each individual has associated with it a spatial location which represents its activity center (or home range center), and which is unknown. The collection of these activity centers is thought as the realization of a statistical point process, a class of probability models for characterizing the spatial pattern and distribution of points (Illian, 2008). A first spatial component of this point process describes how individuals are distributed in a predetermined area called the state-space.

A second observation component models how individuals are detected, considering the location of their activity center and the location of the traps. It is referred as the encounter probability model in which the capture data *y* of an observed individual *i* at a trap *j* in occasion *k* is a Bernoulli random variable (i.e., y = 1 if captured and 0 otherwise):

$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k}).$

In the half-normal encounter model, the most basic and commonly used model, the capture probability $p_{i,j,k}$ is assumed to decrease with the distance between an individual activity center (*s_i*) and the trap location (*x_j*):

$$p_{i,j,k} = p_{0,j,k} \times e^{\frac{-\|s_i - x_j\|^2}{2\sigma^2}}.$$

This model introduces two key parameters for the SCR model: the baseline capture probability p_0 , which is the probability of detecting an individual at the exact location of its activity center (i.e., $s_i = x_j$); and the spatial scale parameter σ which controls the rate of decrease in capture probability as a function of the distance between s_i and x_j . These two parameters can be related to different individual or spatial covariates, such as the sex or the type of trap location, to account for potential heterogeneity in capture.

There are several key assumptions when using SCR models. Firstly, the population studied needs to be demographically closed, which means that no birth or death occurred during the sampling period. The population also needs to be geographically closed: no permanent emigration or immigration occurred but temporary movements are allowed, resulting in variable spatial exposure to capture, which is specifically considered in SCR models. Secondly, the activity centers of the individuals are assumed to be randomly distributed in the study area. Finally, the capture events should have occurred independently within and among individuals, trap locations and occasions (Borchers & Efford, 2008; Efford et al., 2009; Royle et al., 2014, 2018; Sutherland et al., 2019).

2. Input data and state-space

Two files were required as input data: the encounter data file (edf), a frame containing all the capture events per individual, per 24 hour-occasion and per camera trap, with the information about the sex for each individual (Appendix 1); and the trap deployment file (tdf), a frame containing for each of the 88 camera traps its identification name, its spatial coordinates, the days when it was operational for the duration of the study (i.e., trap operability), and the type of trap location as a covariate (i.e., marking site, road, other). In details, 24 camera traps were set at marking sites, 55 on roads and nine at other locations which included salt licks and water places (Appendix 2). Similarly to the other studies on lynx population size estimation using SCR models, a capture occasion was subsequently defined as five consecutive days (Pesenti & Zimmermann, 2013; Avgan et al., 2014; Weingarth et al., 2015; Kubala et al., 2019; Gimenez et al., 2019; Dul'a et al., 2021; Palmero et al., 2021; Iosif et al., 2022), resulting in a total of 49 occasions. The functions created for discretizing the *edf* and *tdf* are presented in Appendix 3, along with the function to determine the number of distinct individuals captured per sex and the total number of recaptures (i.e., the total number of captures minus the number of distinct individuals captured). *oSCR* package includes some data checks, such as if all the camera traps in the *edf* are mentioned in the *tdf*, and calculates the average number of captures per individual and of spatial locations where individuals were encountered at, with the *data2oSCR()* function. These parameters are simple measures of the sampling size.

Another prerequisite input of the model is the definition of the state-space, which represents the possible locations of the activity centers of individuals that might be captured in the study area. Therefore, this state-space needs to be large enough so that no individual outside of this area has any probability of being captured. A common way to define it is by buffering the trap array. A general rule of thumb is to apply a buffer width of three to four times the estimated spatial scale parameter σ from the half normal encounter model and a resolution of half the σ value. As σ was not known *a priori*, it was approximated with half of the mean maximum distance moved (*mmdm*) which is the average for all recaptured individuals of the furthest distance between the multiple locations they were captured. The *data2oSCR()* function in oSCR allows for its calculation. In this study, the *mmdm* was equal to 10.8 km, hence σ was set as 5.4 km. oSCR includes the possibility to automatically generate a state-space by referring the buffer width around the trap locations and the resolution of the grid. Another option is to create a personalized state-space by removing the areas of unsuitable habitat for the species studied. In this study, the methodology used was to create a personalized state-space with QGIS (QGIS.org, 2022), combining the delimitation of the lynx territory in Croatia with a buffer around the camera trap locations (Figure 1). In addition, the area corresponding to the sea was removed from the state-space. It was recommended to test a range of buffer width and resolution values to confirm that parameter estimates were insensitive to the choice of values (Sutherland et al., 2019).

3. Model implementation and ranking

Firstly, null models, i.e., without covariates, have been fitted for testing the sensitivity of the estimates to different values of buffer width and resolution, as mentioned in the previous paragraph. The different buffer widths tested ranged from 14.5 to 26.5 km with an increment

of two kilometres, along with the delimitation of the lynx territory (Figure 1). The polygons defined with QGIS were imported in R using the *sf* package (Pebesma, 2018) and following the script described in the *oSCR* vignette book (Dupont et al., 2022). Two rules were followed when choosing the adequate buffer width: (1) they were considered large enough as soon as the SCR density estimate per pixel stabilized, as commonly recommended (Royle et al., 2014); (2) the abundance estimate should be superior to the minimum population size of 69 individuals (Gomerčić et al., 2021). Therefore, the 16.5 km and the 22.5 km buffer widths were chosen according to the first rule only and both rules respectively (Figure 3) and are referred as the 16.5 km state-space and the 22.5 km state-space below.



Figure 3: SCR estimates of density per pixel (+ 95% CI) and abundance (+ 95% CI) of lynx for null models with increasing size of the state-space.

The threshold of the minimum population size previously estimated in Croatia is shown (Gomerčić et al., 2021).

For the resolution, two values were tested: 0.5 and 0.25 of the σ value for the 22.5 km buffer width. As the null model with a $0.25*\sigma$ resolution took a greater amount of time to run and yielded an inconsistent result for the abundance, the $0.5*\sigma$ resolution was selected.

A test for different values of *trimS* was also needed. Indeed, this argument is defined as a "non-negative value with the same distance units as traps [that] performs a local evaluation". It is often needed to speed computation and to integrate variable trap operability (Sutherland et al., 2019). Null models were fitted for the 22.5 km state-space with values of *trimS* ranging from 21 to 27 km with an increment of two kilometres. The 23 km value was selected for the rest of the analysis as the density estimate was equal to the density estimate without the *trimS* set.

After setting the state-space and the *trimS*, seven models were fitted for both statespace, differing in the combination of covariates (sex and location_type) used for modelling the baseline capture probability p_0 and the spatial scale parameter σ (Table 1). Especially, the models including the sex as a covariate of σ and not of p_0 (model_covs3, model_sex3) were supported by the study on the lynx population in Central Europe (Palmero et al., 2021) and the results of Sarmento & Carrapato (2019) for the Iberian lynx (Lynx pardinus). Along with the null model, the models were ranked based on the Akaike Information Criterion differences (dAIC) (Burnham et al., 2002). Predicted values of density per 100 km², abundance, p_0 and σ were produced using the *get.real()* function implemented in *oSCR* for a list of selected models in order to highlight the influence of the integration of covariates on the estimates. This list included the best model within the ones that integrated either both covariates, either the sex or the location type alone, along with the null model (Table 1). For converting the density per pixel into the two demographic parameters of interest, the *d.factor* argument of the function was set at ~13.7 for predicting the density per 100 km², as the resolution of the state-space was equal to ~2.7 x 2.7 km² (i.e., $0.5*\sigma$), and at the number of pixels contained in each state-space for predicting the abundance.

When sex information is included in the data object, as it was in this study, *oSCR* uses by default a particular form of likelihood which accommodates observed and missing sex data. The probability that an individual in the population is a male ψ is then estimated along with the other parameters of the model. Therefore, the sex-ratio, expressed as the logit-scale of ψ , was calculated for each model. Sex-specific demographic parameters (i.e. density and abundance) were also estimated (Royle et al., 2015; Sutherland et al., 2019).

III. Results

A. Camera trapping and lynx identification

Due to technical reasons, such as camera trap failures, dead batteries, programming errors, snowfall and sabotage, the sampling effort was reduced to 14,400 trap-days.

The discretization of the data removed six capture events resulting in eighty-eight capture events in total for the sampling period. The total number of distinct independent individuals identified was 31, including individuals identified by both sides and by their right side only, and was not impacted by the discretization of the data. The sex was successfully determined for 27 individuals (15 females and 12 males), leaving only four unknown-sex individuals. Lynx were captured on 1 to 10 occasions with an average number of capture events per individual of 2.84 and an average number of spatial locations where individuals were encountered at of 1.52. In total, 57 recapture events occurred representing 18 individuals captured more than once (Appendix 4).

B. SCR analysis

1. Comparison between the two state-spaces

The topmost parsimonious SCR model for both state-space included the location type as a covariate of the baseline capture probability p_0 and the sex as a covariate of the spatial scale parameter σ (Table 1). For the 16.5 km state-space, the predicted density of lynx per 100 km² (95% CI) was 0.89 (0.59-1.36) and the predicted abundance (95% CI) was 104 individuals (69-160) divided in 78 females and 26 males. For the 22.5 km state-space, the predicted density of lynx per 100 km² was 1.01 (0.65-1.59) and the predicted abundance was 141 individuals (90-221) divided in 110 females and 31 males. The baseline capture probability p_0 per type of location (95% CI) were similar between the two state-spaces and were the following for the 16.5 km state-space: 0.119 (0.065-0.207) for the marking sites, 0.019 (0.010-0.037) for the roads and 0.028 (0.007-0.110) for other types of location. The spatial scale parameter σ (95% CI) was also similar between the two state-spaces and were the following for the 16.5 km statespace: 4,703 km (3,805-5,812) for the males and 2,584 km (2,081-3,208) for the females. The estimates for the other models were similar between the two state-spaces (Figure 4, Table 2a&b).

Table 1: Model selection results for fitted SCR models ranked by AIC for the two state-spaces. Models for which estimates were produced for comparison are highlighted in orange.

	Model		Model R name	dAIC (16.5 km)	dAIC (22.5 km)
D~1	p0~location_type	σ~sex	model_covs3	0	0
D~1	p0~sex+location_type	σ~sex	model_covs1	1.3	1.4
D~1	p0~sex+location_type	σ ~1	model_covs2	14.2	14.8
D~1	p0~1	σ~sex	model_sex3	18.7	18.2
D~1	p0~location_type	σ ~1	model_loctype	18.8	18.9
D~1	p0~sex	σ~sex	model_sex1	19.8	19.3
D~1	p0~sex	<u>σ~1</u>	model_sex2	32.6	33.0
D~1	p0~1	<u>σ~1</u>	null_model	35.5	35.9



Figure 4: SCR estimates of density per 100 km² (+ 95% CI) and abundance (+ 95% CI) of lynx for each selected model and with the two state-spaces.

Table 2a: SCR estimates of the capture probability p_0 , the spatial scale parameter σ and the sex ratio for each selected model with the 16.5 km state-space.

Baseline capture probability p_0					Spatial	scale p	Sex-ratio			
Ectimate	SE	95% CI	95% CI	Sex	Estimato	СЕ	95% CI	95% CI	(logit-scale probability	
LSumate	SE	lower	upper		Estimate	SE	lower	upper	of being a male)	
	Marki	ng site								
0.119	0.035	0.065	0.207	f	2584	285	2081	3208		
	Ro	ad							0.26	
0.019	0.007	0.010	0.037						0.20	
	Ot	her		m	4703	508	3805	5812		
0.028	0.020	0.007	0.110							
0.063	0.013	0.042	0.004	f	2724	326	2155	3444	0.27	
0.005	0.015	0.042	0.074	m	4868	471	4027	5885	0.27	
Marking site										
0.091	0.025	0.053	0.153							
Road					4018	345	2206	1751	0.44	
0.017	0.006	0.008	0.033	-	4010	545	5590	4734	0.44	
Other										
0.024	0.017	0.006	0.094							
0.052	0.011	0.035	0.078	-	4208	341	3590	4932	0.44	
	Baselin Estimate 0.119 0.019 0.028 0.063 0.063 0.091 0.091 0.017 0.017	Baseline captur Estimate SE 0.119 0.035 0.119 0.035 0.019 0.007 0.019 0.007 0.020 0.0013 0.063 0.013 0.0051 0.0051 0.0052 0.017 0.0152 0.011	Baseline capture probabi SE 95% CI lower SE 95% CI lower 0.007 0.007 0.119 0.035 0.065 0.019 0.007 0.010 0.028 0.020 0.007 0.063 0.013 0.042 0.091 0.025 0.053 0.017 0.005 0.053 0.017 0.008 0.008 0.017 0.008 0.008 0.017 0.008 0.008 0.017 0.0063 0.017	Baseline capture probability p₀ Marking probability p₀ 0.019 0.035 0.0653 0.207 0.019 0.007 0.010 0.037 0.019 0.007 0.010 0.037 0.010 0.007 0.010 0.037 0.028 0.020 0.007 0.110 0.029 0.013 0.024 0.094 0.017 0.006 0.003 0.033 0.017 0.006 0.003 0.033 0.017 0.0017 0.006 0.094 0.0152 0.011 0.035 0.078	Baseline capture probability p_0 Set is probability p_0 Estimate SE 95% CI lower 95% CI upper Sex Marking site 0.019 0.035 0.065 0.207 f O.019 0.035 0.207 f O.019 0.007 0.0037 f O.019 0.007 0.010 0.037 m O.010 0.037 0.013 f O.010 0.037 m O.010 0.007 0.110 f O.013 0.042 M m O.013 0.042 f O.013 0.094 f O.017 0.006 0.0033 f O.017 0.006 0.0034 f O.011 0.035 0.078 f	Baseline capture probability p_0 Spatial Baseline capture probability p_0 Sex Spatial Baseline capture probability p_0 Sex Spatial Baseline capture probability p_0 Sex Estimate Marking site Ar03 0.019 0.007 0.010 Sex Estimate Marking site Ar03 O.010 0.037 f 2584 O.019 0.007 O.0037 F O.010 0.037 MarKing site O.025 O.033 O.110 f 2724 Marking site F 4018 O.017 O.025 O.033 O.153 O.017 O.026 O.078 4018	Baseline capture probability p_0 Spatial scale p_1 SE 95% CI lower upper Sex Markiew site Toto Colspan="4" Sex Sex Sex 0.019 0.035 0.020 Sex Sex Sex 0.017 0.007 0.035 Sex Sex 0.023 0.035 Sex Sex 0.023 0.035 Sex Sex <th colspan="</td> <td>Baseline capture probability p_0Sex Spatial scale parameterBaseline capture probability p_0Sex Spatial scale parameterMarking scale parameterSex Spatial scale parameterMarking scale parameterMarking scale parameterMarking scale parameterMarking scale parameterMarking scale parameterOuterSex Sex SexBaseline parameterOuterSex SexBaseline parameterOuterSex SexOuterSex SexOuter<th< td=""><td>Baseline capture probability p_0Spatial scale parameter (m)Baseline capture probability p_0Spatial scale parameter (m)Baseline capture probability p_0Spatial scale parameter (m)Baseline capture probability p_0SexBaseline capture (m)SexBaseline capture (m)SexBaseline capture (m)SexBaseline (m)SexBaseline (m)SexBaseline (m)Sex0.013<th c<="" td=""></th></td></th<></td>	Baseline capture probability p_0 Sex Spatial scale parameterBaseline capture probability p_0 Sex Spatial scale parameterMarking scale parameterSex Spatial scale parameterMarking scale parameterMarking scale parameterMarking scale parameterMarking scale parameterMarking scale parameterOuterSex Sex SexBaseline parameterOuterSex SexBaseline parameterOuterSex SexOuterSex SexOuter <th< td=""><td>Baseline capture probability p_0Spatial scale parameter (m)Baseline capture probability p_0Spatial scale parameter (m)Baseline capture probability p_0Spatial scale parameter (m)Baseline capture probability p_0SexBaseline capture (m)SexBaseline capture (m)SexBaseline capture (m)SexBaseline (m)SexBaseline (m)SexBaseline (m)Sex0.013<th c<="" td=""></th></td></th<>	Baseline capture probability p_0 Spatial scale parameter (m) Baseline capture probability p_0 Spatial scale parameter (m) Baseline capture probability p_0 Spatial scale parameter (m) Baseline capture probability p_0 SexBaseline capture (m) SexBaseline capture (m) SexBaseline capture (m) SexBaseline (m) SexBaseline (m) SexBaseline (m) Sex0.013 <th c<="" td=""></th>	

Table 2b: SCR estimates of the capture probability p0, the spatial scale parameter \sigma and the sex ratio for each selected model with the 22.5 km state-space.

	Baseline capture probability p_{θ}					Spatial	scale	Sex-ratio			
Model (R name)	Ectimato	СЕ	95% CI	95% CI Sex		Estimato	СЕ	95% CI	95% CI	(logit-scale probability	
	Estimate	SE	lower	upper		LSumate	SE	lower	upper	of being a male)	
		Marki	ng site								
	0.117	0.033	0.066	0.198	f	2307	357	1703	3123		
D ~1 p0 ~location_type σ ~sex		Ro	ad							0.22	
(model_covs3)	0.020	0.007	0.010	0.039						0.22	
		Ot	her		m	4769	503	3878	5863		
	0.029	0.021	0.007	0.115							
D ~1 p0 ~1 σ~sex	0.065	0.014	0.042	0.007	f	2573	352	1968	3365	0.26	
(model_sex3)	0.003	0.014	0.042	0.097	m	4856	471	4015	5873	0.20	
	Marking site										
	0.091	0.025	0.052	0.155							
D ~1 p0 ~location_type σ ~1	Road					1038	350	3407	1785	0.44	
(model_loctype)	0.017	0.006	0.008	0.033	-	4030	550	5407	4705	0.44	
	Other										
	0.024	0.017	0.006	0.095							
D ~1 p0 ~1 σ~1	0.052	0.011	0.025	0.079		1218	242	2508	4046	0.44	
(null_model)	0.052	0.011	0.055	0.078	-	4210	542	5598	4940	V.44	

2. Comparison between the different models

The comparison of the estimates between the different models was consistent between the two state-spaces. According to the AIC differences, the models that integrated both the sex and the location type as covariates (*model_covs*) were the top ranked models, before the models with only one of the two covariates (*model_sex*, *model_loctype*) and the null model. Moreover, the model integrating the location type covariate alone (*model_loctype*) was of similar rank as the models integrating the sex covariate alone (*model_sex1* and *model_sex3*). In parallel, the integration of the sex as a covariate of p_0 did not have a significant influence on the estimates (*model_covs1* versus *model_covs3*, *model_sex1* versus *model_sex3*), which was also supported by the high AIC difference of the model integrating only the sex as a covariate of p_0 (*model_sex2*) (Table 1).

Density per 100 km² and abundance estimates varied greatly between the different models, especially between the null model and the top one. The estimates also increased, along with their 95% CI, with the number of covariates integrated (Figure 4). The sex-ratio was biased towards females for all models. For p_0 and σ on the contrary, estimates were quite similar between the different models, with high overlapping 95% CI (Table 2a&b). The baseline capture probability p_0 was higher at marking sites and similar between the roads and other locations. For σ , males had higher values that were equal to approximately the double of the female ones.

IV. Discussion

The abundance and density estimates obtained with camera trapping data and SCR modelling in this study accounted for the size of the lynx population in Croatia before the start of the reinforcement process undertaken by the LIFE Lynx project in 2019. According to the state-space used and the covariates included in the models, the estimates were greatly different.

A. Definition of the state-space

One major advantage of the SCR models over the non-spatial CR models is that they integrate the spatial nature of the sampling method relative to the spatial distribution of the animals studied. The definition of the state-space is a key element to account for this spatial information and can be different from the study area: while the latter refers to the region within which the population of interest lives, the former needs to include all the individuals that might have been captured by the sampling method. Therefore, the commonly recommended rule

when defining the state-space is to choose a buffer width around the study area that is large enough to include all animals with non-negligible probability of being captured. In concrete terms, this translates into a stabilization of the density estimates (Royle et al., 2014). For example, Pesenti & Zimmerman (2013) chose a 15 km buffer width around their trap array after testing 10 different buffer widths ranging from 1 to 19 km and observing that the density estimates stabilized after 9 km. However, the abundance estimate remains sensitive to the expansion of the state-space as it is calculated by multiplying the density per pixel with the number of pixels contained in the state-space. This observation motivated the application of a second rule when defining the state-space in this study. Contrary to other lynx populations in Europe, the minimum population size in Croatia was known (Gomerčić et al., 2021). Therefore, the second state-space was chosen for which the density estimates stabilized and that yielded an abundance estimate superior to the minimum population size. When considering the top SCR model, the difference in the abundance estimates between the two state-spaces was of 39 individuals with 95% CI slightly overlapping. Few studies focused on the performances of SCR models to estimate abundance. Blanc et al. (2013) carried out a simulation study with several scenarios comparing different capture probabilities and population sizes, and analyzed a real dataset from a camera trapping study on the lynx in the French Jura Mountains. In comparison with non-spatial CR models, they showed that the SCR model tended to overestimate the abundance for two scenarios, including the one that mimicked the lynx dataset (i.e., a small population with a low capture probability). The explanation they proposed for this positive relative bias was because of the individuals that moved out or partially out of the trapping array, creating an inflated estimate of abundance. However, they did not provide any information about the extent of the state-space they used. In another study, Efford & Fewster (2013) tested the influence of the spatial extent of sampling on population size estimates, using data from simulations and from a field study on skink with pitfall trapping. When comparing the abundance estimates from SCR models for two hypothetical regions of interest: the polygon formed by joining the perimeter traps and the region within 20 m of at least one trap; they found that the estimates with the latter state-space was the double of the estimates with the former. They argued that extrapolation beyond the sampled region was risky and that when inference is required for a large region it is preferable to extend the sampling design. In fact, one particularity of the lynx monitoring in Croatia is the extent of the study area (9,501 km²) which is considerably wider than other study areas in Europe (Table 3).

Region, COUNTRY	Length and timing of the sampling period	Study area size (km ²)	Density estimate (number of independent lynx per 100 km ² suitable habitat)	Regional abundance (number of independent lynx)	
North-Western Alps,	1 Dec 2007 - 30 Jan 2008 (60 days)	2 800	1.47 (SD 0.25)	22 (SE 1.01)	
SWITZERLAND	27 Nov 2009 - 26 Jan 2010 (60 days)	2,800	1.38 (SD 0.23)	23 (SE 0.76)	
Ciglikara Nature Reserve, TURKEY	30 Nov 2010 - 2 Feb 2011 (65 days)	1,028.25	4.20 (95% CI = 2.33-6.22)	Estimated posterior mean lynx population size: Nsuper = 43.27	
Štiavnica Mountains Protected Landscape Area, SLOVAKIA	Western portion: 6 Jan - 6 Mar 2014 (60 days) Eastern block: 16 Mar - 14 May 2014 (59 days)	776	0.58 (SD 0.13)	9 (SE 3.74)	
Veľká Fatra National Park, SLOVAKIA	4 Dec 2014 - 2 Feb 2015 (59 days)	665	0.81 (SD 0.29)	7 (SE 0.54)	
Jura Mountains, FRANCE	Seven sessions from Jan 2011 to May 2015 (58 to 99 days each)	-	Between 0.24 (SE 0.02) and 0.91 (SE 0.03)	Between 5 (SE 0.1) and 29 (SE 0.2)	
Western Carpathians, CZECH-SLOVAK- POLISH borderland	Five sessions (2015 - 2019) from Nov to Feb each (80 days)	1,609	Between 0.26 (SD 0.07) and 1.85 (SD 0.35)	Between 3.63 (SD 0.99) and 18.68 (SD 3.50)	
Bohemian-Bavarian Forest, AUSTRIA- CZECH-GERMANY borderland	Ten sessions (2009 - 2018) from 15 Sep to 24 Dec each (100 days)	760	Between 1.09 (SE 0.35) and 2.36 (SE 0.79)	Between 47.94 (SE 11.03) and 121.25 (SE 42.45)	
Southern Carpathians,	17 Dec 2018 - 31 Mar 2019 (105 days)	1 000	1.60 (SE 0.39)	44.12 (SE 8.48)	
ROMANIA	9 Oct 2019 - 16 Jan 2020 (100 days)	1,200	1.73 (SE 0.38)	48.06 (SE 8.11)	

Table 3: Sampl	ing design.	estimates and	l methods used	for other	SCR studies o	on lvnx po	pulations in Europe.	
				<i>Je. e</i> ,		··· · · · · · · · · · · · · · · · · ·	P · · · · · · · · · · · · · · · · · · ·	

Capture probability in suitable habitat	Spatial scale parameter σ (km)	Methods used for the presented results	Reference
0.013	4.53	Density & σ : SCR modelling using the R package <i>SPACECAP</i> (Gopalaswamy et al., 2012) (Bayesian estimation with data augmentation)	Pesenti &
0.073	4.38	Abundance & capture probability: CR modelling (model M0) with the CAPTURE module in the program <i>MARK</i> (White & Burnham, 1999)	2013
0.214 (95%CI = 0.152-0.290)	2.90 (95%CI = 2.24-3.67)	SCR modelling using the R package SPACECAP (Bayesian estimation with data augmentation)	Avgan et al., 2014
0.101 (SD 0.028)	6.42 (SD 0.86)	Density, capture probability & σ : SCR modelling using the R package <i>SPACECAP</i> (Bayesian estimation with data augmentation) Abundance : CR modelling (model Mb) with the CAPTURE module in	Kubala et al., 2019
0.033 (SD 0.012)	5.47 (SD 1.74)	the program MARK	
Between 0.05 and 0.11	Between 5.12 and 7.9	SCR modelling using the R package <i>oSCR</i> (Maximum likelihood estimation)	Gimenez et al., 2019
Between 0.02 (SD 0.01) and 0.22 (SD 0.06)	Between 3.17 (SD 0.69) and 9.83 (SD 0.44)	SCR modelling using the R package SPACECAP (Bayesian estimation with data augmentation) (no mention of the method used for estimating the population size)	Dul'a et al., 2021
Between 0.00 (SE 0.00) and 0.02 (SE 0.00)	<u>Females:</u> between 1.7 (SE 0.3) and 4.3 (SE 0.4) <u>Males:</u> between 3.0 (SE 0.3) and 5.2 (SE 0.5)	SCR modelling using the R package <i>secr</i> (M. Efford, 2022) (Maximum likelihood estimation)	Palmero et al., 2021
-	3.310	Density, abundance & capture probability : SCR modelling using the R package <i>secr</i> (Maximum likelihood estimation)	
-	3.343	σ : root pooled spatial variance function as a measure of the 2D dispersion of the locations where individuals were detected	Iosit et al., 2022

It was therefore understandable that in the present study, an increase of six kilometers of the state-space increased widely the abundance estimates and raised greater concerns about the definition of the state-space. One solution to refine the state-space could be to remove unsuitable habitat for lynx, such as human settlements, intensively used agriculture lands or lakes (Avgan et al., 2014; Kubala et al., 2019). Sollmann et al. (2011) recognized that it can influence movement and density estimates in SCR modelling but it still remains an arbitrary approach, unless the areas that animals do and do not use are certain. Zimmermann (2004) developed a GIS probability model, based on habitat information and radio-telemetry data from the lynx population in the Swizz Jura Mountains. The elevation, the slope, forest areas and roads were selected among the 18 predictors tested as the best ones to explain the presence/absence of the lynx. However, Zimmermann underlined the local nature of the models and recommended their application only to regions similar to those where the basic data used were originally gathered. Lynx demography and distribution can also be greatly influenced by prey availability. Herfindal et al. (2005) have been able to predict variations in the home-range size of the lynx in Norway with an index map of prey density established with the reported number of prey kills by hunters. This relation could have only been made by assuming that the harvest density of prey reflected the population density. The authors recognized that this assumption appeared to be valid in Norway because of the organization of the hunting system in the country. Therefore, data on number and distribution of lynx preys could be an important predictor of lynx ecological parameters but are still not available in adequate form or precision to be incorporated into a habitat model. Moreover, Efford & Fewster (2013) showed that SCR estimates were relatively robust to misspecification of the density model and that a homogeneous model still provided reliable estimates. The present study highlights the need to define more precise guidelines when defining the state-space in SCR modelling, especially when the abundance is required.

B. Integration of covariates

The integration of covariates yielded great differences in the estimates, especially for the abundance and the density. Between the null model and the top model, estimates were almost the double, with low overlapping 95% CI and an upper value that exceeded 200 individuals for the top model with the 22.5 km state-space, a relative high number compared to field observations (i.e., genetics, mortality, etc.). While knowing abundance estimates are important for management purposes and assessing the conservation status of a population,

density estimates allow for comparison between different study areas. The lynx density in Croatia seemed to be in the lower range of the estimates from other lynx populations in Europe (Table 3). However, several factors in this study could make the comparison with other studies questionable and one of these is the integration of covariates. All the other studies on the lynx did not include covariates, except one which included the sex (Palmero et al., 2021). In their study on the lynx population from the French Jura and Vosges Mountains, Gimenez et al. (2019) found that sex-specific SCR analyses produced unreliable abundance and density estimates, which might be due to the high number of unknown sex individuals. The intensive monitoring of the lynx conducted in Croatia for multiple years improved the knowledge on individual's identity and could explain the relative low number of unknown sex individuals in this study. In a simulation study, Royle et al. (2015) showed that not using the sex information because of missing data clearly biased the estimates. To ignore the sex information is to ignore the associated heterogeneity in capture probability. To solve this issue, they developed a formulation of the likelihood, implemented later in oSCR, that accommodates missing sex information and allows models with and without class structured parameters to be compared by AIC with or without these missing information (Sutherland et al., 2019). The inclusion of the sex as a covariate in SCR models is all the more important in the case of felids as sexes differed greatly in their behavior and space use (Sollmann et al., 2011). In a recent study on the lynx in Central Europe, they surprisingly found no significant difference across sexes for both the baseline capture probability p_0 and the spatial scale parameter σ . The given explanation for the first parameter was that females with kitten hunt at a higher rate which can result in a similar activity level to males. For σ , the restricted and seasonal sampling period could have been not appropriate for annual home range estimation, and the detection of many non-resident individuals could have biased these estimates (Palmero et al., 2021). On the contrary, in the present study, males had a significantly higher σ value than females, which is in accordance with the known ecology of the lynx. In their study on the Iberian lynx, Sarmento & Carrapato (2019) also found that the top model was the one that included the sex as a covariate of σ only and that males had a higher value than females. Interestingly, in the present study, the model that included the type of location alone was of similar rank as the models that included the sex only, resulting in similar estimates of density and abundance. This suggest that none of these two covariates were more informative than the other and that the estimates would be same if just one of them was available, i.e. datasets with only the sex information or the type of location information. Though, it would be very unlikely because the sex is an informative feature of the structure of a population and camera traps are not usually placed at random locations. Therefore,

further SCR analysis should integrate the sex as a covariate, especially for species showing sexspecific behavior and space use. Moreover, even though studies are already using particular locations for camera traps, further investigations on the integration of such trap-level covariates are needed to understand their influence on parameter estimates.

C. Estimates precision and potential sources of bias

The 95% CI associated with the estimates were particularly wide in this study, limiting the reliability of the demographic estimates for the lynx population in Croatia. For critically endangered species, this unreliability could have dramatic consequences in the decisions for future conservation plans.

One important assumption of SCR models is the demographic and geographical closure of the population, i.e., no birth/death or immigration/emigration occurred in the population during the sampling period, which can be tested with the CloseTest program (Stanley & Richards, 2005, 2011). The geographical closure is assured by defining the state-space large enough to include all the animals that could have a non-zero probability of being captured and that could have moved temporarily outside of the study area. However, this assumption can be violated by subadults which are by definition non-resident animals in phase of dispersal, and hence not part of the population studied. The subadults can not be distinguished from resident lynx (i.e., adults), unless their historical background is known, i.e., they have been photocaptured the previous year as kitten. As it is rarely the case, the bias caused by the subadults can be reduced by choosing a sampling period outside of the dispersal season, which mostly starts between March and May, with a peak in April (Zimmermann et al., 2005). Most of the other studies on the lynx in Europe sampled for 60 days during the winter season (Table 3), based on the first lynx population size estimations led in Switzerland (Zimmermann et al., 2007, 2013). This relatively short sampling period associated with the biological seasonality of the lynx species allowed for the population studied to be considered as demographically closed and to benefit from a higher capture probability. Indeed, no birth occur during this time as the birth season takes place during May/June (Breitenmoser-Würsten et al., 2001) and the chances of a lynx dying over this short period of time are low. The winter season also corresponds to the pre-mating season in which lynx from both sexes are making larger and more frequent movements, which can increase the capture probability (Breitenmoser-Würsten et al., 2001; Zimmermann et al., 2013). With rare and elusive species, there is a need to find a compromise between sampling for short enough so that the closure assumption is not likely to be violated,

but long enough to gather sufficient data to provide reliable estimates. Open population models, as opposed to closed population models, allow for additions (i.e., birth, immigration) and/or losses (i.e., death, emigration) in the studied population over the sampling period, and hence provide a more efficient way to integrate multiple years or sessions of sparse data that are likely to violate the closure assumption. While closed population models only provide size estimates of a static population, open population models can give an insight into the processes that drive population changes by additionally estimate vital rate such as survival and recruitment rates (Gardner, Reppucci, et al., 2010; Royle et al., 2014; Glennie et al., 2019). However, several factors have limited the use of these relatively new models, including model complexity and computational constrains. Moreover, even if they relax the assumption of population closure, they still have other assumptions, such as individual movement patterns, that can affect parameter estimation (Gardner et al., 2018). In their study, Palmero et al. (2021) used both open and closed population SCR models and showed that open models had the ability to deal with incomplete detection data which resulted in biased estimates in the case of closed models. However, Weingarth et al. (2015) argued that the existing closure tests might not be appropriate in case of low number of captures in the data collected. They suggested that maximizing the number of recaptures should be weighted higher than meeting the assumption of demographic closure. A threshold of 20 recaptures was recommended by Efford et al. (2009) in order to get precise estimates. Therefore, based on the number of sufficient recapture events, the detection probability and the precision of the density estimates, the most adequate sampling period for the camera-trapping session was defined to last at least 80 days from late summer (i.e., beginning of September) until beginning of winter (i.e., mid-November) (Weingarth et al., 2015). In their simulation study, Dupont et al. (2019) supported the lengthening of the sampling period because it increased the sample size (i.e., the number of distinct individuals captured and the number of spatial recapture events), and hence the precision of population size estimates, while reducing the bias associated with sparse SCR data. However, in the case of intermediate and fast life history species, the relative bias and the associated standard deviation increased when the sampling period was overlapping the reproductive period. Therefore, they recommended to extend the sampling period as much as practically/economically feasible, while avoiding sampling during recruitment times. In the present study, the sampling period was defined as to avoid the birthing months and the dispersal period, leading to an unprecedented study length of 244 days. So even if the closure tests did not validate the closure assumption in this study (results not shown), the population could still be reasonably considered as closed. The consistent data collection was made possible by the intensive and extensive

camera-trap monitoring set up in Croatia under the LIFE Lynx project. At the end of this project in 2024, fewer camera traps and human resources are to be expected. An optimal timeframe needs to be defined, as not only the length of the sampling period is important, but also the timing. Indeed, in a one-year SCR analysis on a jaguar (*Panthera onca*) population, Harmsen et al. (2020) showed that density estimates fluctuated through time in relation with behavior. In some instances, a shift of only one 24-hour occasion between two 3-month survey periods resulted in a doubling of the density estimates. They warned about the use of relatively short sampling period when comparing demographic estimates between sessions as the variations will reflect behavioral changes rather than a real change in population size. A similar analysis using the moving-window method can be applied to the data collected in Croatia to define the optimal timeframe for the future camera trapping surveys.

Increasing numbers of distinct individuals captured and recaptures can arise from a maximized capture probability. In traditional CR methods, a minimum capture probability of 0.3 was recommended to get reliable estimates (White et al., 1982) but was almost never reached. One solution considered to increase the capture probability, and that all the studies on the lynx population in Europe applied, was to use discrete sampling occasions by defining one occasion as five consecutive days. Indeed, for wide ranging species living at low densities, 24 hour-occasions can result in zero-heavy encounter histories. Pooling occasions may eliminate more zeros than ones and then increases the overall capture probability in order to meet a minimum value of 0.1 (Foster & Harmsen, 2012). Even if the benefits were not demonstrated, discrete occasions were used in SCR analysis of lynx populations for standardization reasons (F. Zimmermann, pers. com.). In the present study, the discretization of the data removed only six captures events out of the 94 in total. However, the capture probability outreached the 0.1 minimum value at marking site only. Low capture probabilities are a common feature in lynx population analysis (Table 3). Moreover, as pooling can still reduce the number of capture events, especially for short sampling periods, and introduces subjectivity over the length of the occasions, continuous-time SCR models have been developed, in which there are no longer occasions but a continuous survey (Borchers et al., 2014; Dorazio & Karanth, 2017). While using the full information contained in the data, the authors did not find as many benefits as expected in estimating population density compared to discrete-time models (G. Distiller, pers. com.).

The spatial survey design is a critical element in getting reliable estimates as it directly influences the sample size. In a study on the effects of the size of the area surveyed on CR and SCR estimates, Zimmermann et al. (2013) showed that SCR models were more robust to

changes in trap array size and were able to make reliable predictions of density as long as sufficient data were collected across a certain range of distances. They recommended a minimum trap array of 760 km² for lynx CR studies. One of the most important aspects is then to choose camera trap locations that maximize the probability of capturing the focal species, especially for the rare and elusive ones that live at low density. In the case of the lynx, camera traps are often place at the edge of forest paths, roads and trails, based on previous signs of lynx presence (e.g., footprints, hair) and on local knowledge (Zimmermann et al., 2007, 2013; Kubala et al., 2019; Gimenez et al., 2019; Dul'a et al., 2021; Palmero et al., 2021; Iosif et al., 2022). Preliminary surveys proved to be an efficient way to identify these optimal locations with the possibility of moving the camera traps with very low capture probabilities (Avgan et al., 2014; Royle et al., 2014). The present study demonstrated that marking sites were also favorable locations for capturing lynx with camera traps. However, as the resident males tend to visit the same marking sites that belong to their territory, it can result in added heterogeneity in capture probability between the sex and can violate the assumption of independence between capture events for one individual. Moreover non-resident males might be attracted by marking sites (Vogt et al., 2014), which can lead to a positive bias in population size estimates.

Along with the location of the traps, the space between them is important. Traditional CR surveys require that no individual in the study area have a zero-probability of been captured which can be achieved by avoiding any holes in the trap array that could contain an animal's entire home range. Therefore, the trap spacing needs to be on the same order as the radius of a typical home range or possibly of the smallest home range recorded for the study species in the study area or a similar area (Royle et al., 2014). To ensure a consistent coverage of the entire area of interest, the common method used is to divide the study area into grid cells, the size of which approximates an average home range, and to place one trap within each or every second cell. Females lynx have smaller home range compared to males, which range between 106 to 832 km² according to the study area, the highest been estimated in Norway (Herfindal et al., 2005). A 2.7 x 2.7 km grid was commonly applied in lynx studies based on the first studies in Switzerland (Zimmermann et al., 2007, 2013). Because of the large extent of the study area in Croatia, its topography and the economical and resource limitations, camera traps were placed according to a 10 x 10 km grid. By assuming a bivariate normal model for detection (i.e., the half-normal encounter model), the estimated spatial scale parameter σ can be converted into a 95% home-range radius estimate, which represents the distance from the home-range center within which 95% of the points of the state-space are used by the animal (Pesenti & Zimmermann, 2013; Royle et al., 2014). Using the following R script: $\sigma^*(qchisq(0.95,2)^{0.5})$;

and the smallest σ value estimated (i.e., 2,307 m for the females in the 22.5 km state-space), the smallest 95% home-range radius in this study was 5,647 m. The buffering of the locations of the camera traps with this distance revealed many holes in the investigation of the study area, i.e., possible lynx territories not covered with camera traps (Appendix 5). However, these holes are of no concern in SCR analysis because by explicitly defining the state-space, models can make predictions outside the range of the data, i.e., for the individuals living in these holes. Moreover, not only the numbers of distinct individuals captured and of recaptures are important in SCR analysis, but also the spatial recaptures, i.e., recaptures at multiple locations. Smith et al. (2020) warned that SCR estimates obtained with repurposed data from non-spatial CR design were not reliable because CR surveys are not specifically designed for maximizing this number of spatial recaptures. A trade-off in design arises between spreading the traps out as much as possible that should yield the most distinct individuals captured, but probably few spatial recaptures, and having a lot of traps very close together that should produce the most spatial recaptures but very few distinct individuals captured (Royle et al., 2014). Based on a simulation study, Sollmann et al. (2012) showed that SCR models performed well as long as the extent of the trap array was similar to or larger than the extent of individual movements during the study period and as long as σ was at least half the average distance between traps. In the present study, the first condition was met but not the second one where camera traps were spaced wider than the recommendation (Appendix 5). This can explain the relatively low value for the average number of spatial locations where individuals were encountered at (i.e., 1.52). In SCR modelling, while the total number of distinct individuals captured and of recaptures are informative about the baseline capture probability, spatial recaptures are informative about the spatial scale parameter σ . However, it is possible to directly estimate σ from telemetry data alone. Therefore, the integration of this type of data into SCR analysis can compensate the lack of spatial recaptures, even if data are available for few telemetered individuals only (Royle et al., 2013). Moreover, it has been demonstrated that the use of telemetry data can increase the precision of parameter estimates, as it accounts for the heterogeneity in capture probability resulting from the heterogeneity in resource distribution in the landscape and hence in space use by individuals. This new class of model combining SCR and telemetry data allows to integrate more realistic patterns of space use directly into SCR models and avoid bias in estimating population size. Linden et al. (2018) completed the combined model developed by Royle et al. (2013) in order to accommodate the lack of independence between the data sources, as the telemetered individuals can also be photo-captured by camera traps, and was later implemented into the oSCR package. As underlined before, the study area for the lynx

monitoring in Croatia largely exceeded the extent of the other studies, resulting in a relatively low number of spatial recaptures. Further analyses integrating telemetry data could improve the precision of the parameter estimates for the lynx population size in Croatia.

V. Conclusion

This study estimated the pre-reinforcement size of the lynx population in Croatia, based on camera trapping data and SCR analysis. These estimates are important as the comparison with estimates from subsequent monitoring sessions will provide an assessment of the success of the reinforcement process that started in 2017 under the LIFE Lynx project, with the first translocations of lynx in 2019. To confirm the critical status of this population in Europe, the density estimates seemed to be in the lower range of the estimates from other studies on the lynx. However, important considerations over the definition of the state-space and the integration of covariates in the models are to be investigated for adequate comparison. Moreover, the estimates were associated with a high level of imprecision that could limit their usefulness in decision making for conservation purposes. Further analysis over the specific sampling design, in terms of timing and spatial scale, and the integration of telemetry data are needed to optimize the monitoring of the lynx in Croatia and obtain reliable population size estimates.

VI. Supplementary data

The following files are joined to this report:

- R project,
- *edf* (edf_min_2019-2020.csv),
- *tdf* (tdf_2019-2020.csv),
- custom function scripts (Functions.txt),
- GIS files for the state-spaces (lynx territory, DIYss_14.5 26.5km)
- R script,
- R data associated.

I advise you to not run the models as it can take a great amount of time, depending on the power of your computer. The results of the models are integrated in the R data.

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Appendix 1: Extract of the *edf*

Thirty first lines of the *edf* containing the individual identification (*individual_name*), the occasion (occasion_ID) and the trap (trap_ID) at which the individual was captured, its sex (sex_ID; F for female, M for male and U for unknown) and the number of the session (session_ID, only one in this study). The structure of the corresponding data in R are given below.

individual_name	occasion_ID	trap_ID	sex_ID	session_ID
CRO231	91	CRO326_3	F	1
CRO327	188	CRO278_1	М	1
CRO329_3	46	CRO329_1	F	1
CRO329_3	147	CRO329_3	F	1
CRO329_3	166	CRO329_3	F	1
CRO329_3	208	CRO329_2	F	1
CRO329_3	214	CRO329_3	F	1
CRO329_5	35	CRO329_1	U	1
CRO372_1	125	CRO372_1	F	1
Crno jezero 2	63	CRO504_1	F	1
Crno jezero 2	137	CRO504_1	F	1
Crno jezero 3	28	CRO504_1	F	1
Fulir	35	CRO504_1	U	1
Fulir	155	CRO504_1	U	1
Goran ZIP L09	177	CRO375_1	М	1
Goran ZIP L09	189	CRO375_1	М	1
Goran ZIP L09	20	CRO446_5	М	1
Goran ZIP L09	61	CRO446_3	М	1
Goran ZIP L09	134	CRO417_3	М	1
Goran ZIP L09	145	CRO446_3	Μ	1
Goran ZIP L09	175	CRO446_3	М	1
Goru	205	CRO329_2	М	1
Jela LCRO21	88	CRO326_3	F	1
Jela LCRO21	102	CRO326_3	F	1
Jela LCRO21	167	CRO326_3	F	1
Kira	198	CRO418_1	F	1
Kira	206	CRO446_3	F	1
L13 Velebit	16	CRO551_1	F	1
L13 Velebit	146	CRO551_8	F	1

> str(edf) #structure of the data

'data.frame': 94 obs. of 5 variables:

\$ individual_name: Factor w/ 31 levels "?ina","Crno jezero 2",..: 4 5 6 6 6 6 6 7 8 2 ...
\$ occasion_ID : int 91 188 46 147 166 208 214 35 125 63 ...
\$ trap_ID : Factor w/ 24 levels "CRO231_1","CRO278_1",..: 3 2 4 6 6 5 6 4 7 15 ...
\$ sex_ID : Factor w/ 3 levels "F","M","U": 1 2 1 1 1 1 1 3 1 1 ...
\$ session_ID : int 1 1 1 1 1 1 1 1 1 ...

Appendix 2: Extract of the tdf

Twenty first lines of the *tdf* containing the trap identification (*trap_station_name*), the X and Y coordinates of their location in the Universal Transverse Mercator (UTM) system (*UTMx*, *UTMy*), the trap operability (matrix of zeros and ones for the length of the sampling period; 1 if operational, 0 if not), one column of separation (*sep*) between the trap information and the covariate (*location_type; marking_site, road, other*). The structure of the corresponding data in R are given below.

trap_station_Name	UTMx	UTMy	1	2	3	4	•••	241	242	243	244	sep	location_type
CRO231_1	351499.18	5044202.68	1	1	1	1		1	1	1	1	/	marking_site
CRO276_1	339466.83	5040111.15	1	1	1	1		1	1	1	1	/	marking_site
CRO277_1	343459.511	5043692.12	1	1	1	1		1	1	1	1	/	marking_site
CRO277_2	343103.091	5037717.43	1	1	1	1		1	1	1	1	/	marking_site
CRO278_1	354258.25	5036789.46	1	1	1	1		1	1	1	1	/	marking_site
CRO280_1	372486.558	5031339.81	1	1	1	1		1	1	1	1	/	marking_site
CRO280_2	376602.837	5040690.26	1	1	1	1		1	1	1	1	/	road
CRO326_2	357512.648	5023281.52	1	1	1	1		1	1	1	1	/	marking_site
CRO326_3	355430.85	5029752.05	1	1	1	1		1	1	1	1	/	marking_site
CRO327_1	360533.919	5030220.71	1	1	1	1		1	1	1	1	/	marking_site
CRO329_1	381854.522	5029771.46	1	1	1	1		1	1	1	1	/	road
CRO329_2	379760.798	5021981.54	1	1	1	1		1	1	1	1	/	marking_site
CRO329_3	385025.756	5021638.49	1	1	1	1		1	1	1	1	/	marking_site
CRO372_1	367365.328	5018836.58	1	1	1	1		1	1	1	1	/	marking_site
CRO372_2	364143.229	5017582	1	1	1	1		1	1	1	1	/	marking_site
CRO374_1	380021.071	5018794.45	1	1	1	1		1	1	1	1	/	marking_site
CRO375_1	391050.013	5011424.32	1	1	1	1		1	1	1	1	/	marking_site
CRO375_2	389345.649	5018918.23	1	1	1	0		0	0	0	0	/	marking_site
CRO416_1	364543.793	5008527.76	1	1	1	1		1	1	1	1	/	road
CRO417_3	375490.285	5007267.12	0	0	0	1		1	1	1	1	/	marking_site

```
> str(tdf[,1:7]) ; str(tdf[,244:249]) #structure of the data
'data.frame': 88 obs. of 7 variables:
$ Trap_Station_Name: Factor w/ 88 levels "CR0231_1","CR0276_1",..: 1 2 3 4 5 6 7 8 9 10 ...
$ UTMx
                 : num 351499 339467 343460 343103 354258 ...
$ UTMy
                 : num 5044203 5040111 5043692 5037717 5036789 ...
                 : int 1111111111...
$ X1
                 : int 1111111111...
$ X2
$ X3
                 : int 1111111111...
$ X4
                 : int 1111111111...
  ...
$ X241
              : int 1111111111...
$ X242
              : int 1111111111...
$ X243
              : int 1111111111...
$ x244
              : int 1111111111...
              : Factor w/ 1 level "/": 1 1 1 1 1 1 1 1 1 ...
$ sep
$ location_type: Factor w/ 3 levels "marking_site",..: 1 1 1 1 1 1 1 3 1 1 1 ...
```

Appendix 3: Custom functions

}

```
discrete.edf<-function(edf, occasion_length){</pre>
  #Takes an edf and discretizes the occasions of Length occasion_Length
  edf$occasion_ID <- sapply(edf$occasion_ID/occasion_length, FUN = ceiling)
#divides edf$occasion_ID by occasion_length and takes the upper integer
  edf$indocc <- paste(edf$individual_name, edf$occasion_ID) #creates a new
column with individual_name and the number of the occasion concatenated
  print(c(nrow(edf) - length(unique(edf$indocc)), "(", nrow(edf), "-",
length(unique(edf$indocc)), ")", " capture events will be deleted."), quote =
FALSE)
  edf <- edf[!duplicated(edf$indocc),] #removes the duplicated lines
according to the column indocc --> 2 cases:
    #1) Deletes the capture events that occurred more than 1 time at the same
location on the same occasion and keeps just one
    #2) Deletes the capture events of an individual at 2 different locations
for the same occasion and keeps just one over the 2
  edf<-subset(edf, select=-indocc) #deletes the column indocc</pre>
  return(edf)
```

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```
discrete.activity <- function(trap_activity, K, occasion_length) {</pre>
  #K is the real number of occasions ; occasion_length is the length of one
occasion ; trap_activity is a line of a data_frame with K columns containing
the information about activity of ONE trap
  #Discretize the activity of one trap (trap activity) from K occasions to
K/occasion length occasions
  if ((K/occasion_length)%%1 == 0 ) {
                                         #K is a multiple of occasion_length
    dis_trap_activity <- rep(0, times = (K/occasion_length))</pre>
    for (i in seq(occasion length, ncol(trap activity), occasion length)) {
      if (unique(paste(trap_activity[,(i-occasion_length+1):i]))[1] == "1" |
isTRUE(unique(paste(trap_activity[,(i-occasion_length+1):i]))[2] == "1")) {
        dis trap activity[i/occasion length] <- 1</pre>
      }
    }
  }else { #K is NOT a multiple of occasion_length ==> we will treat the last
interval apart
    k <- (round(K/occasion length)-1) #number of intervals of length</pre>
occasion length
    last_interval <- ncol(trap_activity) - k * occasion_length #length of</pre>
the last interval
    dis_trap_activity <- rep(0, times = k + 1)</pre>
    for (i in seq(occasion_length, k * occasion_length , occasion_length)){
      if (unique(paste(trap_activity[,(i-occasion_length+1):i]))[1] == "1" |
isTRUE(unique(paste(trap_activity[,(i-occasion_length+1):i]))[2] == "1")) {
        dis_trap_activity[i/occasion_length] <- 1</pre>
      }
    }
    #Last interval
    if (unique(paste(trap_activity[,(K-last_interval):K]))[1] == "1" |
isTRUE(unique(paste(trap_activity[,(K-last_interval):K]))[2] == "1")) {
      dis_trap_activity[k+1] <- 1</pre>
    }
 }
 return(dis_trap_activity)
}
discrete.tdf<-function(tdf, K, occasion_length){</pre>
  #K is the real number of occasions ; occasion_length is the length of one
discrete occasion
  #Discretizes the activity of all the traps of the tdf from K occasions to
K/occasion_length occasions
  dis traps activity (-data.frame()
  for (i in 1:nrow(tdf)){
    dis_traps_activity<-rbind(dis_traps_activity,</pre>
discrete.activity(tdf[i,4:(4+K-1)], K, occasion_length)) #Columns 4:(4+K-1)
as the information about the trap activity is after the name and coordinates
of the traps (first 3 columns) and before covariates
  }
  colnames(dis traps activity)<-1:(round(K/5))</pre>
  dis_tdf <- data.frame(tdf[,1:3], dis_traps_activity, tdf[,(4+K):ncol(tdf)])</pre>
  return(dis_tdf)
}
```

```
recap.count<-function(edf, K){</pre>
 #Calculates the number of captures per individual, the number of different
individuals captured and recaptured, ant the total number of recaptures all
individuals combined
 history_matrix <- history.matrix.alldata(edf, K)</pre>
 #Number of captures per individual with the sex information
 captures <- data.frame(rowSums(history_matrix))</pre>
 unique <- edf[!duplicated(edf$individual_name),] #unique values of</pre>
individual names
  captures <- data.frame(captures, unique$sex_ID)</pre>
 names(captures)<-c("nb_captures", "sex")</pre>
 print(captures)
 nb_female <- length(unique$sex_ID[unique$sex_ID=="F"]) #number of females</pre>
 nb_male <- length(unique$sex_ID[unique$sex_ID=="M"]) #number of males</pre>
 nb_unknown <- length(unique$sex_ID[unique$sex_ID=="U"]) #number of unknown
sex individuals
 ", nb_female,
                                     , nb_male,
        "\n", "Number of unkonwn sex: ", nb_unknown))
 #Number of different individuals captured and recaptured
 nb_ind_recaptured<-0
 nb_recaptures<-0
 for (i in 1:nrow(captures)){
   if(captures$nb_captures[i]>=2){
     nb_ind_recaptured<-nb_ind_recaptured+1</pre>
     nb_recaptures<-nb_recaptures+captures$nb_captures[i]-1 #-1 because I
don't want to count the first capture
   }
 }
 cat(c("\n", "\n", "Total number of captures (all individuals together): ",
sum(captures$nb_captures),
        "\n", "Total number of recaptures (all individuals together): ",
nb_recaptures,
        "\n", "Number of distinct individuals captured: ", nrow(captures),
        "\n", "Number of distinct individuals recaptured (captures >=2): ",
nb_ind_recaptured,
        "\n", "Number of distinct individuals captured only once: ",
nrow(captures) - nb_ind_recaptured))
```

}

Appendix 4: Sample size

data<-data2oscr(edf= edf,	#encounter data file
tdf=list(tdf),	#a list of tdf with one for each session
sess.col=5,	#session column (edf)
id.col=1,	#individual column (edf)
occ.col=2,	#occasion column (edf)
trap.col=3,	#trap column (edf)
<pre>sex.col=4,</pre>	#optional: sex column (edf)
<pre>sex.nacode="U",</pre>	#unknown sex code
K=49,	#number of occasions
ntraps=nrow(tdf),	#number of traps
trapcov.names="locati	ion_type", #covariate names

tdf.sep="/") #character used as separator between the trap characteristics (ID and coordinates) and the covariates

```
#scrFrame
sf <- data$scrFrame
sf #numerical summary
              51
n individuals 31
n traps
              88
n occasions
             49
                      S1
avg caps
                    2.84
avg spatial caps
                    1.52
mmdm
                10803.21
```





recap.count(ed	df,49)				
	nb_captures	sex			
CR0231	1	F			
CR0327	1	М			
CR0329_3	5	F			
CR0329_5	1	U			
CR0372_1	1	F			
Crno jezero 2	2	F			
Crno jezero 3	1	F			
Fulir	2	U			
Goran ZIP L09	7	М			
Goru	1	М			
Jela LCRO21	3	F			
Kira	2	F			
L13 Velebit	2	F			
L9 Velebit	5	M			
Lipa	1	F			
Mali	5	U			
Marko ZIP L16	5	М			
Marta	4	F			
Miška	2	F			
Novi Ri?i?ko	1	F			
Paul	3	M			
Pa?o	5	M			
R6	1	U			
Rista L18	1	M			
Saša	1	M			
Silvia	1	F			
Spot	10	F			
Stipe L20	2	M			
Vilim	2	M			
Zarez	9	м			
?ina	1	F			
Number of fe	males: :	15			
Number of ma	les: :	12			
Number of un	konwn sex:	4			
Total number	of captures	(all	individuals together): 88		
Total number	of recaptur	es (a	11 individuals together): 57		
Number of di	fferent indi	vidua	ls captured: 31		
Number of di	fferent indi	vidua	ls recaptured (captures >=2):	18	
Number of in	dividuals ca	pture	d only once: 13		

Appendix 5: Buffers around the camera trap locations

The camera trap locations were buffered with the minimum σ value estimated in this study (i.e., 2,307 m) and the calculated 95% home-range radius (i.e., 5,647 m) in order to highlight the holes in the monitoring of lynx in its distribution in Croatia.

