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A decade of monitoring the critically endangered Balkan lynx in its core area: Insights from spatial capture recapture models

Dime Melovski [a,1], Inès Moreno [b,*,1], Aleksandar Stojanov [a], Aleksandar Pavlov [a], Andrej Gonev [a], Vasko Avukatov [a], Yon Halotel-Diez [c], Gjorge Ivanov [d], Fridolin Zimmermann [b,e]

[a] *Macedonian Ecological Society, Skopje, North Macedonia*
[b] *KORA, Carnivore Ecology and Wildlife Management, Ittigen, Switzerland*
[c] *Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences, Elverum, Norway*
[d] *Geonatura, Zagreb, Croatia*
[e] *Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland*

A R T I C L E I N F O

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A B S T R A C T

Monitoring the status of endangered species is essential to guide conservation and management measures, especially for populations facing isolation and small numbers. The Balkan lynx (*Lynx lynx balcanicus*), the most endangered subspecies of the Eurasian lynx, survives in the south-western Balkans with fewer than 50 mature individuals. Obtaining accurate population estimates is challenging for such a rare, wide ranging and elusive species. We used camera-trapping and Spatial Capture-Recapture (SCR) modelling to provide the first reliable density estimates of the Balkan lynx in its core area, Mavrovo National Park and surroundings, over a decade-long monitoring period. Across five sessions, we recorded 176 detections over 9439 realised camera trap nights, identifying up to 10 individuals per session. Despite a low number of recaptures, our multisession analyses reveal a decline in density (SE) over the past decade, from 2.3 (± 0.7) lynx per 100 km^2 of suitable habitat in 2013 to 1.2 (± 0.4) in 2023. We compared densities estimated independently for each session or as a trend, with and without excluding unsuitable habitat. These findings provide the first robust density estimates for the critically endangered Balkan lynx and confirm concerns about the state of the population. Our results underscore the value of long-term, systematic monitoring to detect changes in population density. While density estimates are comparable to other lynx populations in Europe, the observed decline, combined with the genetic state of the population, highlights the urgent need for enhanced conservation efforts.

1. Introduction

Understanding demographic parameters, such as population size, density and their trend over time is essential for the effective conservation and management of many species, especially threatened ones (Williams et al., 2002; Udevitz and Gould, 2014, Fležar et al., 2023). However, estimating demographic parameters of large carnivores, such as population size, density, trends, survival and

* Corresponding author.
E-mail address: i.moreno@kora.ch (I. Moreno).
[1] Both authors contributed equally to the manuscript

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turnover, is particularly challenging due to their vast home ranges, low densities, and nocturnal, secretive behavior, which contribute to low detection rates (Obbard et al., 2010).

Advancements in digital camera traps have profoundly revolutionised field biology, providing a non-invasive method to monitor wildlife in any spatiotemporal condition (Rovero and Zimmermann, 2016; Weingarth et al., 2015). The integration of Spatially Explicit Capture-Recapture (SCR) models with camera trapping has become a standard approach for assessing demographic parameters in many wild felids with distinctive coat patterns (e.g. Greenspan et al., 2020). SCR models evolved from traditional Capture-Recapture (CR) models and, by accounting for animal movement and location relative to the trap array, eliminate the need to calculate the effective sampling area (Efford and Fewster, 2013; Sollmann, 2018; Marrotte et al., 2022, Palmero et al., 2023a). Multisession extensions of SCR have also been developed to analyze multi-year or multi-season data under a consistent framework (e.g., Gardner et al., 2010; Royle et al., 2014; Efford, 2025a). These approaches allow explicit modeling of changes in density or demographic parameters over time for assessing population trends.

In the present study we focus on the Balkan lynx (*Lynx lynx balcanicus*), a distinct subspecies of the Eurasian lynx. Once widespread throughout the peninsula, the Balkan lynx is now restricted to the mountainous regions along the border of North Macedonia, Albania and Kosovo (Kaczensky et al., 2024). It is also sporadically found in southern Montenegro (von Arx et al., 2004, Melovski et al., 2018). The last expert-base estimate indicates that no more than 50 mature individuals are left in the wild, rendering it the most critically endangered subspecies of Eurasian lynx in the world (Melovski et al., 2015). In addition to its small population size, the Balkan lynx faces threats from habitat loss, poaching, genetic isolation and high recent inbreeding, which limit its range and compromises genetic diversity (Gonev, 2025; Melovski et al., 2021). Conserving this rare and endangered subspecies demands scientifically robust data to effectively plan and implement conservation and management measures across all range countries (Bonn Lynx Expert Group, 2021). Until 2006, there had been no field studies conducted on this critically endangered subspecies, resulting in a scarcity of data primarily reliant on expert judgement and estimates (Breitenmoser-Würsten, Breitenmoser, 2001). Since then, assessments of the Balkan lynx's status were carried out on the population level and through the implementation of the Balkan Lynx Recovery Programme, providing a more comprehensive understanding of its conservation needs (Melovski et al., 2021).

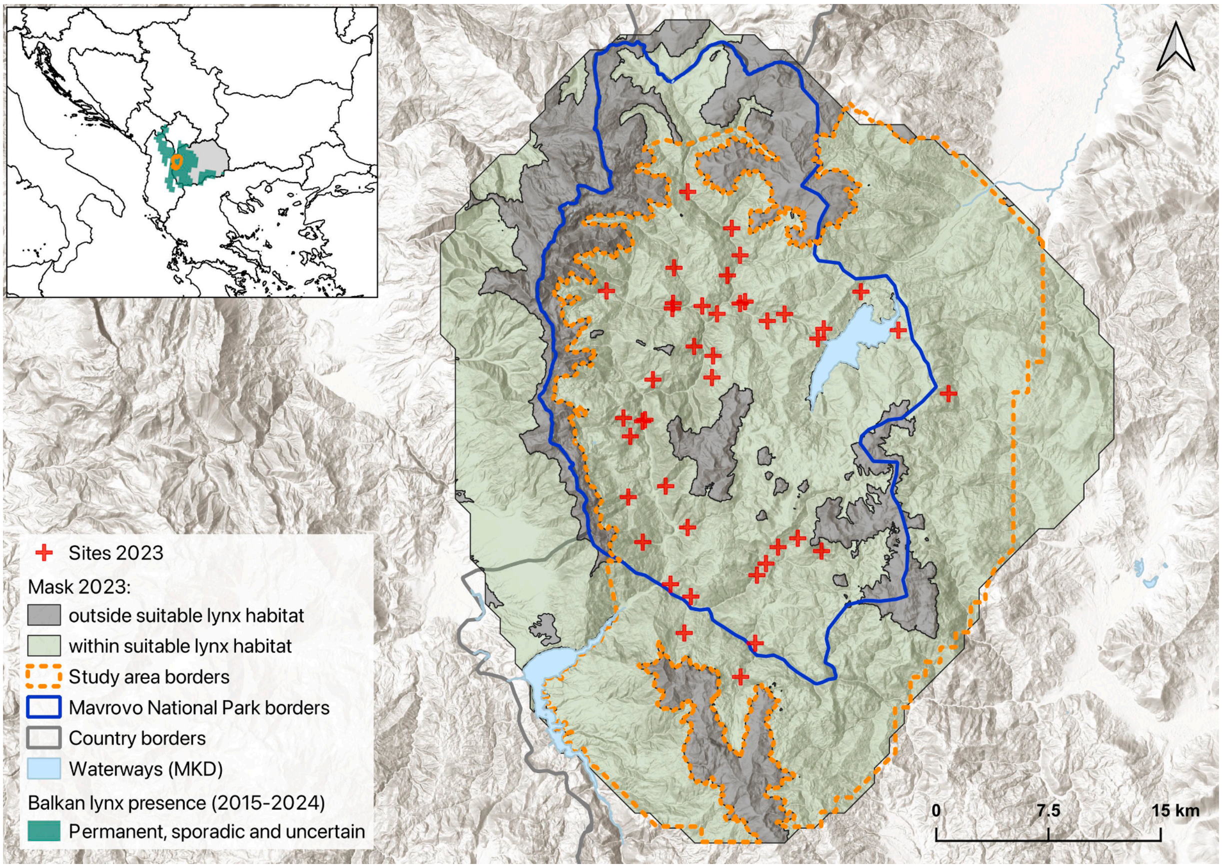

Fig. 1. Study area in North Macedonia (orange polygon, 1012 km2 of suitable habitat). The borders of Mavrovo NP (blue polygon) are shown along with the camera trap locations (red crosses) used during the 2023 session. The 2023 mask (buffer strip = 11.6 km) is shown, with habitat areas deemed suitable for lynx depicted in green and excluded areas in black. Excluded habitats include lakes, areas above 1800 m altitude and populated places with more than 5000 inhabitants. Country borders are displayed for spatial reference. Maps and buffer strips for the other sessions are provided in Supplementary Material, Fig. S1.

In this context, we applied the photographic capture-recapture method for the first time in the Mavrovo National Park. This approach had already been successfully used to study Eurasian lynx in various regions of Central and Western Europe (e.g., Pesenti and Zimmermann, 2013; Weingarth et al., 2015; Kubala et al., 2019; Dul'a et al., 2021; Fležar et al., 2023). Our initial pilot study from 2008 demonstrated the feasibility of this method for monitoring the elusive Balkan lynx, providing the first reliable population estimates and insights into individual movement patterns (Melovski et al., 2008). Given the species' critically endangered status and the need to track population trends over time, we repeated the camera-trapping surveys five times between 2013 and 2023. This long-term monitoring allowed us to assess population stability, refine our statistical methodology and sampling design, and inform future conservation strategies.

In this paper, we present the first SCR estimates of the abundance, density, and trend for the Balkan lynx in Mavrovo NP and its surrounding areas in North Macedonia, a core area for this species (Melovski et al., 2021). For this purpose, we considered five systematic camera-trapping sessions conducted over a 10-year period (2013–2023). Specifically, we aim to determine the density and number of Balkan lynx in this core area and to examine how this population has changed over time, identifying any potential trends.

2. Material and methods

2.1. Study area

The study area encompasses Mavrovo NP (lat. 41.7030, lon. 20.6635), the largest NP in North Macedonia, covering a total of 737 km^2, and its adjacent areas (Fig. 1). Located in the western part of the country, within the Scardo-Pindic mountain range, the area includes parts of the Shara, Korab, Deshat and Bistra mountains. Elevations range from 600 m in river valleys to 2764 m at Mount Korab's peak. The region is characterised by diverse forest types, including beech, oak, fir, and mixed forests, along with subalpine and alpine pastures. The human population density is estimated at 3.5–10 individuals per km^2, making it one of the least populated regions in the country with high emigration rates (State statistical office of the Republic of Macedonia, 2022).

Approximately 45 % of the Mavrovo NP area is forested. Of this, over 70 % consists of broadleaved forests, predominantly European beech (*Fagus sylvatica*) and various oak species (*Quercus* spp.). Mixed forests make up more than 18 % of the area, primarily beech-fir combinations. Shrublands cover nearly 10 %, and coniferous trees, including Macedonian fir (*Abies borisii-regis*) and European spruce (*Picea abies*), account for around 1 % (Ivanov et al., 2018). Besides the Eurasian lynx, three other large carnivore species occur in the area: brown bear (*Ursus arctos*), grey wolf (*Canis lupus*) and golden jackal (*Canis aureus*). Ungulates are represented by the roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*) and wild boar (*Sus scrofa*) (Melovski et al., 2022). The prevalent climate in the area is mountainous with subtle Mediterranean influences along Radika River (Filipovski et al., 1996).

Being a protected area for over 75 years, Mavrovo NP is considered the core area of the lynx with most findings coming from the park and a stable prey population (Melovski et al., 2018). While traditional livestock grazing and forestry remain the dominant human activities, expanding tourism and infrastructure development increasingly fragment the available habitat for wildlife.

2.2. Sampling design

Camera traps were deployed during the winter and spring of 2013, 2015, 2018, 2021 and 2023. The study area was overlaid with a grid of 2.5 × 2.5 km cells, adjusted from other Eurasian lynx studies aiming at estimating densities with capture-recapture and aligned with the international 10x10km UTM/WGS84 grid (zone 34 N) (Zimmermann et al., 2013). Grid cells with more than two-third of their area above 1800 m were discarded (Melovski et al., 2020). These cells were removed for biological and logistic reasons, as lynx rarely

Table 1
Main characteristics and results of the camera trap sessions conducted in 2013, 2015, 2018, 2021 and 2023 in the Mavrovo NP and its surrounding areas. Each session includes 12 trapping occasions (five consecutive nights each), totaling 60 trapping nights per session.

	2013		2015		2018		2021		2023	
Period of trap activity	March - May		March - May		February - April		March - May		February - April	
Camera trap array (km^2)	393		334		374		374		435	
Number of sites	32		30		30		30		41	
Realised camera trap nights	1813/1920 (94.4 %)		1779/1800 (98.8 %)		1794/1800 (99.6)		1747/1800 (97.0 %)		2306/2460 (93.7 %)	
Dataset	left	right	left	right	left	right	left	right	left	right
Number of detections	30	29	15	16	19	28	9	6	17	15
Number of detected individuals	10	9	7	7	8	9	3	4	7	6
Number of detections/individual: mean, median (min, max)	3, 2.5 (1, 7)	3.2, 3 (1, 9)	2.1, 2 (1, 5)	2.3, 2 (1, 4)	2.4, 1.5 (1, 5)	3.1, 2 (1, 9)	3, 2 (1, 6)	1.5, 1.5 (1, 2)	2.4, 1 (1, 9)	2.5, 1 (1, 8)
Number of recaptures	20	20	8	9	11	19	6	2	10	9
Number of recaptures/individual: mean, median (min, max)	2, 1.5 (0, 6)	2.2, 2 (0, 8)	1.1, 1 (0, 4)	1.3, 1 (0, 3)	1.4, 0.5 (0, 4)	2.1, 1 (0, 8)	2, 1 (0, 5)	0.5, 0.5 (0, 1)	1.4, 0 (0, 8)	1.5, 0 (0, 7)
Number of spatial recaptures	9	8	5	6	7	9	3	2	7	7
Number of spatial recaptures/individual: mean, median (min, max)	0.9, 0.5 (0, 3)	0.9, 1 (0, 2)	0.7, 0 (3, 1.1)	0.9, 1 (0, 2)	0.9, 0.5 (0, 3)	1, 1 (0, 3)	1, 1 (0, 2)	0.5, 0.5 (0, 1)	1, 0 (0, 5)	1.2, 0 (0, 6)

use habitat above timberline (Breitenmoserürsten et al., 2001) and accessibility for maintenance must be guaranteed. An optimal camera-trap site was chosen in every second grid cell. When it was not possible to find a suitable site in the chosen cell, an ideal spot was selected in an adjacent cell. This camera-trap density and distribution ensured that the area sampled included no gaps that could contain an entire animal's home range (around 150 km^2 for females, unpublished data derived from six radio-collared Balkan lynx females), which is an important requirement of conventional capture-recapture models but not mandatory in spatially explicit models. Camera trap locations were selected either based on previous signs of lynx presence and local knowledge or by selecting optimal sites covering all preselected grid cells. Cameras were strategically placed along predictable paths, forest roads, game paths and hiking trails, to maximise the detection probability of lynx (Blanc et al., 2013; Zimmermann and Foresti, 2016).

In 2013, camera traps were deployed at 32 sites, with subsequent surveys conducted at 30 sites in 2015, 2018, and 2021, and 41 sites in 2023. Each survey lasted 60 days, from late February to early May, with minimal variation in site selection and survey period across sessions (Table 1). For each session, a minimum convex polygon was generated to inform about the extent of the trap deployment (Table 1). The study period was selected to coincide with the lynx mating season, maximizing the likelihood of increased movements, while also avoiding the hunting season of ungulates (01 Oct. - 31 January), to minimize potential disturbances. Two camera traps (with no bait) were deployed at each site to maximise identification chances by photographing both flanks of lynx. We employed the following digital camera-trap models: Capture 3.0 Megapixel Scouting Camera, Ambush, C123, and X-Change Color (Cuddeback®, De Pere, WI, USA), each equipped with passive infrared trigger mechanisms with a ¼ second trigger speed and a xenon white flash. The camera traps were positioned 0.6 m above ground, perpendicular to the track and set to take one to two consecutive images per trigger event, with no delay between successive triggers (approximately 10–30 seconds was needed to recharge the xenon white flash). Camera traps were checked weekly to control functionality, change memory cards and batteries when needed, and remove possible obstructions (e.g., snow or overgrown vegetation).

2.3. Individual identification

Following the recommendations in Choo et al. (2020), each lynx photograph was carefully reviewed by at least two distinct members of the project team, who visually identified individual animals by analysing their unique fur patterns, focusing particularly on the positions of spots or rosettes across the lynx's body (Zimmermann and Foresti, 2016). If no agreement is found between the investigators after more than one trial, it is considered that the individual cannot be identified. This usually happens when the image is of bad quality (e.g. blurred or under/overexposed), not well framed or skewed. Each individual in each session was compared to the known individuals in our database and assigned a known ID or a new ID if it was not previously identified. All captures that could not be confidently confirmed through visual inspection, due to poor picture quality, were excluded from the analyses.

2.4. Data analysis

We used SCR multisession analyses to estimate lynx densities and the number of independent lynx present in the Mavrovo NP, using the R package 'secr' (version 5.2.0, Efford, 2025b). In 'secr', multisession analyses can be conducted to combine data from different time periods or study areas, treating them as separate but related 'sessions'. This approach can improve the robustness of density estimates by pooling data across sessions, particularly when individual captures are sparse or when assessing population dynamics over time (Efford et al., 2009). Given the systematic camera trap sessions conducted over multiple years (2013–2023) in Mavrovo NP and the low number of individuals detected, this long-term approach was essential for examining temporal trends and overcoming the limitations of single-session analyses with few capture-recapture events.

The analyses necessitated the compilation of input files encompassing camera traps deployment details (operational nights of cameras), spatial coordinates of trap locations and detailed capture histories, which track individual animals' detection events across sites and sessions. Following Zimmermann et al. (2013), two juvenile captures were replaced by their mother's ID in the capture history to account only for the "independent lynx" (i.e. residents plus dispersers, or adults plus sub-adults). Due to insufficient data on the sex of the individuals captured, we were unable to incorporate sex as a covariable in the SCR models. As usually done in most European studies, capture events were organised into 12 occasions, each spanning five consecutive nights starting from midday, within the 60 nights study period (Table 1), facilitating comparisons of results between studies. In our case we restricted the number of detections of an individual at a particular camera trap site during a sampling occasion to only one detection. Since not all individuals could be identified from both flanks, we conducted separate analyses, one with all left flank photographs and another with all right flank photographs (Kalle et al., 2011; Srivathsa et al., 2015).

A mask (or state space) was also necessary in the models to delineate the geographical bounds for lynx activity centres within the model. We calculated a buffer zone around the trap array using the *suggest.buffer()* function from the 'secr' package, to ensure that no individual animal outside of the area delimited by the corresponding mask has any probability of being detected by the camera traps in the array during the survey. This practice is commonly recommended in spatial capture-recapture studies (e.g., Efford et al., 2004; Royle et al., 2014). To ensure consistency in our analyses, the buffer was calculated on the entire dataset for a given year, allowing us to use the same mask for both left and right flank analyses. By calculating the buffer on the full dataset for each session, we ensure that both flanks are analysed under identical conditions, which is crucial for more comparable results. Analyses were conducted using both a simple mask and a habitat mask (Fig. 1). The habitat mask was applied to refine the model by excluding areas deemed unsuitable for lynx, including lakes, elevations above 1800 m, and urban areas with populations exceeding 5000 inhabitants.

The models were fitted using half-normal function, which considers that the encounter probability is highest when the camera trap site is placed exactly at the animal's activity centre and declines as the distance between camera trap site and activity centre increases based on the kernel of a bivariate normal probability distribution function. Likelihood inference methods were employed to estimate the model parameters. The models were fitted with three primary parameters: density (D), detection probability (g0) and movement parameter (σ). We modelled density with two automatic predictors provided specifically for multi-session analyses: D~**Session** (trend) and D~*session* (independent). The lowercase *'session'* fits a distinct value of the parameter for each session without assuming any relationship between sessions. The initial uppercase '**Session**' fits a trend across sessions using the session number as a continuous predictor. The trend model allows the parameter to vary across sessions while following a common underlying trend across the sessions (random effect) capturing general changes across sessions (Efford, 2025a). Our primary interest lies in the trend model (D~**Session**) for understanding population dynamics over the study period, however, we also conducted the independent analyses (D~*session*) to compare the outcomes of a trend-based and session-specific approach.

We tested various predefined covariables for the detection function parameters to assess how the detection probability g0 is influenced by time effects (*t* for time factor or *T* for time trend), behavioural responses (*b* for learned response, *k* for site-specific learned response, *bk* for individual-by site learned responses), transient responses (*BK* for individual-by site transient responses, *K* for site-specific transient response; Efford, 2022). Sigma was kept constant, assuming consistent movement behaviour across sessions.

For each flank and density parameter ('**Session**' or '*session*') models' selection was conducted using the Akaike Information Criterion (AICc) to account for small sample sizes. Models with a ΔAICc of less than 2 were averaged to provide more robust density estimates. All analyses were conducted in the R programming language (version 5.2.0, R Core Team 2025). The coefficient of variation (CV) for each density estimate was calculated to assess the precision of the results (Palmero et al., 2023a).

To estimate the number of lynx per session within a defined study area (orange polygon in Fig. 1), we multiplied the resulting SCR density estimates (trend model, D~**Session**, suitable habitat mask) by the total area of suitable habitat in that polygon. This study area was defined as a subset of the masks used in the SCR analyses, taking into account important barriers and ensuring that it remained

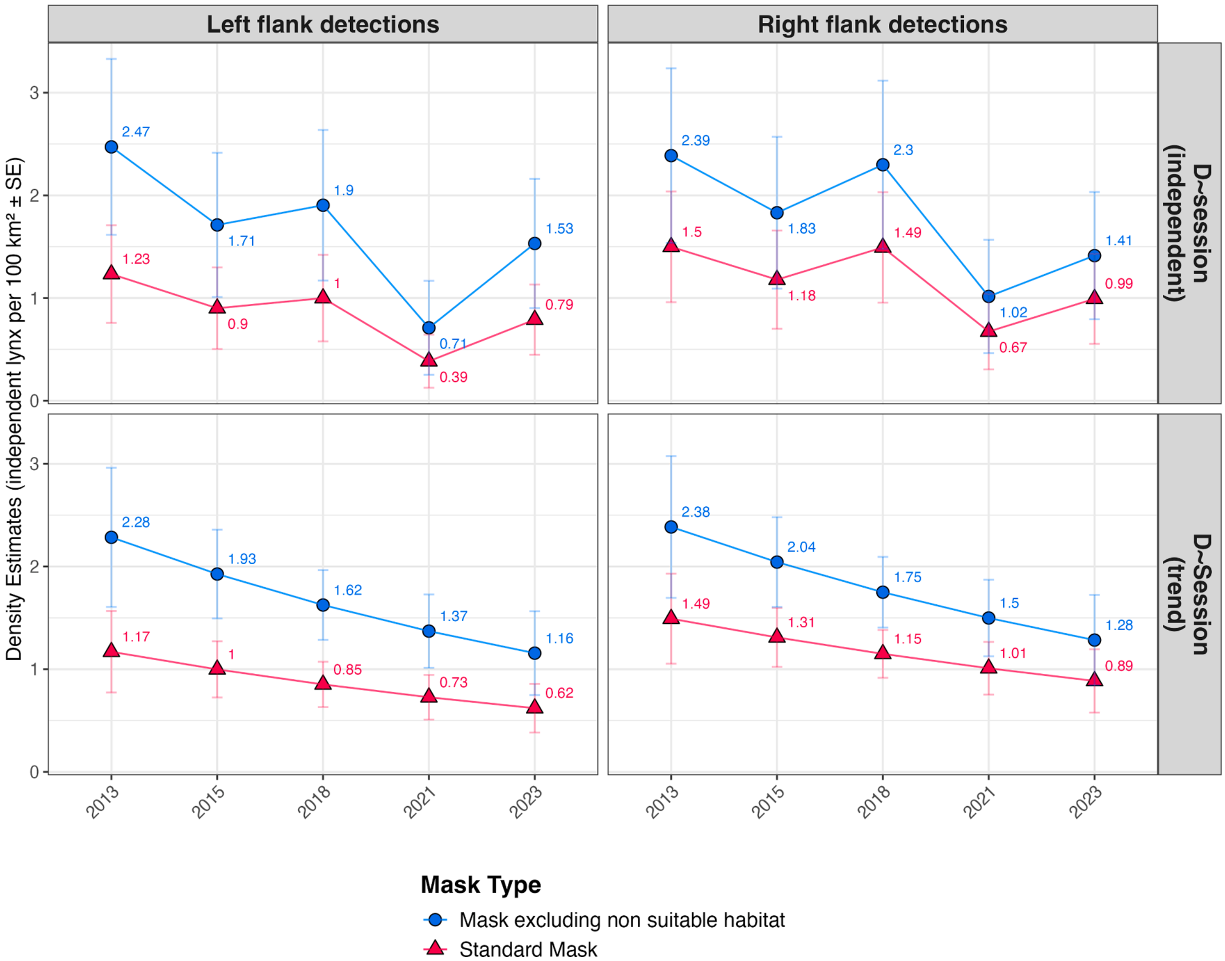

Fig. 2. Estimated lynx densities across sessions for different spatial capture-recapture models. The left panels represent results from the left flank detections, and the right panels from the right flank detections. In the first row, analyses were conducted with a density estimate where the density parameter was modelled as a trend across sessions (D~**Session**). Second row analyses were conducted with density estimates where the density parameter was estimated independently for each session (D~session). Red symbols indicate a standard mask whereas blue symbols indicate a habitat mask. Error bars represent standard errors (SE) for the density estimates.

within the spatial boundaries where density estimates were derived. The portion of the study area extending into Albania was excluded due to the presence of barriers (treeless mountain ridges above 2000 m of altitude). Although occasional movements across these barriers have been observed, such as a radio-collared lynx crossing into Albania and returning, it is unlikely that a lynx would establish a home range spanning both sides of the barriers. The study area was further refined by excluding unsuitable habitats during its delineation and when calculating the number of lynx within suitable habitat. This approach ensured that the abundance estimates reflect the number of lynx residing in suitable habitat within the core area.

3. Results

Due to technical issues and camera theft, the number of potential camera trap nights across various years was reduced. As a result, the realized camera trap nights ranged from 93.7 % to 99.6 % of the total potential nights over the five surveys (Table 1). In total, 176 lynx detections were recorded over 9439 realized camera trap nights.

The number of left and right flank detections for each camera-trapping session is provided in Table 1, with the highest number of left flank detections recorded in 2013 (30 detections, 10 individuals) and the lowest in 2021 (9 detections, 3 individuals). For the right flank dataset, 2018 had the highest number of detections (28 detections, 9 individuals), while 2021 had the lowest (6 detections, 4 individuals) (see Table 1 for details per session).

Multisession analyses of the left flank detections with the standard mask, both with the density parameter estimated independently for each session (D~*session*) and as a trend across sessions (D~**Session**), identified the behavioural responses model bk and k as best fitting models, both with a ΔAICc of less than 2 (Table S1 supplementary material). Consequently, model averaging of these two models was performed to obtain more robust density estimates. However, when excluding unsuitable habitat from the mask, the site-specific transient response K was the best fitting model. Under the trend model (D~**Session**), the estimated density (SE) ranged from 2.28 (± 0.68) independent lynx in 2013–1.16 (± 0.41) independent lynx per 100 km^2 of suitable habitat in 2023. Under the independent model (D~*session*), density estimates ranged from 2.47 (± 0.86) independent lynx in 2013–1.53 (± 0.63) independent lynx per 100 km^2 of suitable habitat in 2023 (see Fig. 2 and Table S2 for full details by session and model).

For the right flank detections, the K model was consistently the best fitting model for both predictors '**Session**' and '*session*', with or without unsuitable habitat excluded from the mask (AICc comparison in the table S1 of the supplementary material). The highest estimate occurred in 2013, with densities (SE) ranging between 2.38 (± 0.69) (trend model) and 2.39 (± 0.85) (independent model) independent lynx per 100 km^2 of suitable habitat, decreasing to values between 1.28 (± 0.44) (trend model) and 1.41 (± 0.62) (independent model) independent lynx per 100 km^2 of suitable habitat in 2023 (see Fig. 2 and Table S2 for full details by session and model).

In both the '**Session**' (trend) and '*session*' (independent) models, with a mask excluding unsuitable habitat, the detection probability (g0) remained stable across sessions, with values of 0.05 (± 0.01) for the left flank dataset and 0.06 (± 0.01) for the right flank dataset. The movement parameter (sigma), kept constant in the models, was estimated at 3.96 km (± 0.35) for the left flank dataset and 3.41 km (± 0.26) for the right flank dataset for the '**Session**' (trend) model excluding unsuitable habitat.

For the '**Session**' (trend) model excluding unsuitable habitat, CV ranged from 20.9 % to 35.3 % for the left flank dataset and from 19.7 % to 34.3 % for the right flank dataset, with detailed values for density, CV, g0, and sigma by analysis type and session provided in Table S2).

For the '**Session**' (trend) model excluding unsuitable habitat, the number of lynx (SE) within the study area ranged from 23.12 (± 6.86) independent lynx in 2013 to 11.7 (± 4.13) independent lynx in 2023 for the left flank, and from 24.14 (± 6.99) independent lynx to 12.99 (± 4.45) independent lynx in 2023 for the right flank (see Table 2 for detailed model-based estimates).

4. Discussion

Using camera traps and SCR models, we conducted the first rigorous population estimation of the Balkan lynx in its core habitat, including Mavrovo NP and adjacent surrounding areas. Our multi-session analysis, spanning a decade, provided crucial insights into population trends and density estimates, allowing us to determine the number of lynx in the core reproductive area and its trend.

Table 2
Estimated number of Balkan lynx (with standard error) in the study area across different sessions and detection models. Population estimates are shown for sessions modelled as a trend or independently and excluding unsuitable habitat.

Year of the study	2013		2015		2018		2021		2023	
Dataset (flank side)	left	right	left	right	left	right	left	right	left	right
Session	23.12 (6.86)	24.14 (6.99)	19.5 (4.37)	20.68 (4.43)	16.45 (3.44)	17.71 (3.48)	13.87 (3.61)	15.17 (3.77)	11.7 (4.13)	12.99 (4.45)
session	25.03 (8.67)	24.17 (8.6)	17.33 (7.11)	18.53 (7.48)	19.27 (7.42)	23.27 (8.29)	7.19 (4.63)	10.29 (5.59)	15.51 (6.37)	14.31 (6.27)

4.1. SCR model outcomes and interpretation

Over the 10-year period, our results showed a general gradual decline across both flank datasets, whether we modelled density as a trend (D~**Session**) or treated each independently (D~*session*).

As both flanks of all detected individuals were not always known, the left and right flank photographs were separated in two datasets to mitigate the bias of incomplete identification on detection probability. The left and right flank analyses yielded similar results and trends, with slightly higher detection rates in certain years (e.g., 2013 and 2018) and somewhat higher density estimates for the right flank dataset compared to the left flank. When we refined the mask by excluding unsuitable habitats the site-specific transient response model (K) was consistently selected as the best-fitting model. A site-specific transient response indicates that the detection probability at a given site changes after the first lynx detection at that site within the same survey session. Unlike a learned response, this effect does not permanently alter behaviour or detection probability beyond that initial encounter - it simply adjusts the probability associated with subsequent detections at that site during the same session. Ecologically, as our parameter estimates suggest an increased detection probability following the first detection event, it may indicate that once a lynx has been detected at a site, the probability of detecting another lynx (or the same lynx again) at that site within the same session is higher. This might reflect consistent use of certain habitat features or travel routes (such as forest roads) that bring lynx back to these camera trap locations. It may also relate to revisiting marking sites, which are often situated along forest roads or natural landmarks. Additionally, the increased movement associated with the mating season may have contributed to higher site revisitation rates during this period. Although our camera traps were placed based on lynx snow tracking and opportunistic camera trapping detections rather than targeting specific marking sites, scent-marking behaviour likely influenced detection patterns, as both males and females mark, with males revisiting marking sites and using forest roads more frequently (Vogt et al., 2014, Krofel et al., 2017). The timing of our surveys, selected to avoid the hunting season and ensure access to remote areas, overlaps with the lynx mating season. This likely contributed to higher detection probabilities but may also have allowed for occasional temporary movements beyond individuals' typical home ranges. One radio-collared lynx was observed crossing the treeless mountain ridges above 2000 m of altitude into Albania and returning, illustrating that such excursions can occur. However, our telemetry data suggest they are rare. In spatial capture-recapture models, this type of behaviour is absorbed into the estimation of the spatial scale parameter σ, which reflects how detection probability declines with distance from an individual's activity centre. Occasional long-distance detections may result in a slightly larger σ, but they do not bias density estimates, which are derived from the number of activity centres located within the defined mask (Royle et al., 2014). Although occasional extraterritorial movements during the mating season may not be fully captured in σ, the relatively low σ values observed in our study indicate that, on average, the individuals detected had limited movement around their activity centres. It is important to acknowledge that some transient or wide-ranging individuals may still have gone undetected or were detected only a few times.

Movement parameters (σ) from our study appear to fall within the lower range of those observed in other Eurasian lynx studies. For example, Zimmermann and Foresti (2016) reported higher σ values of 5.12 km for males and 3.32 km for females, while Kubala et al. (2019) found values between 5.47 km and 6.42 km in the Slovak Carpathians. Duľa et al. (2021) recorded a broader range, from 3.17 km to 9.83 km, depending on site and season. These results could stem from differences in lynx population density and also potentially in different conditions between study areas (e.g. barriers, topography or prey availability).

The distinction between '**Session**' (trend) and '*session*' (independent) in the models reflects different assumptions about density changes across time. In the **'Session'** (trend) models, density was treated as a trend across time, allowing for gradual changes in population densities from one session to the next. In contrast, the *'session'* (independent) models treated each camera trapping session independently, allowing for greater fluctuations in density estimates between sessions. This approach revealed more variability in the results, with densities rising in 2018 and falling sharply in 2021. Such fluctuations are not uncommon in lynx populations and have been documented in other regions, including Switzerland (e.g., Zimmermann et al., 2015, 2016) and the Bohemian-Bavarian Population (e.g., Heurich et al., 2018). These studies report notable interannual variations in lynx densities, often linked to prey availability, human-induced mortality, or dispersal dynamics. In our study, the lower number of effective camera trap nights and detection rates in 2021 may be attributed to factors that remain unclear at this stage. Nonetheless, both modelling approaches consistently indicate an overall decreasing trend in density over the 10-year period.

In view of the low number of detections in 2021, the array size and number of sites has been increased in 2023 to try to increase the number of detections and individuals (Palmero et al., 2023a). While detections almost doubled compared to 2021, the resulting density remained below pre-2021. Under the trend (D~**Session**) model excluding unsuitable habitat, the CV in 2023 was the highest observed (~35 % for both datasets), that may be attributed to the pooling of data across sessions, which exacerbates the influence of declining detection numbers over time, particularly in recent years. While the independent (D~*session*) model showed improved precision compared to 2021, with lower CVs in 2023, its CVs were still higher than pre-2021 levels. This suggests that even if the increased number of sites allowed more detections, it only partially mitigated uncertainty as it could not fully compensate for the low recapture rates and fewer individuals compared to earlier years.

4.2. Limitations

Our study highlights the importance of choosing SCR models to capture the spatial and temporal dynamics of elusive species like the Balkan lynx. However, several limitations must be acknowledged.

While technical challenges, such as camera theft and malfunctions, can theoretically impact the number of effective camera trap nights, potentially influencing detection rates and contributing to data gaps, these issues were minimal in our study and shouldn't have an impact. It is also worth noting that in most of our survey years, we did not meet the commonly suggested threshold of at least 10 individuals and 20 spatial recaptures for SCR analyses (Palmero et al., 2023a). Although this inevitably increases model uncertainty, our decision to use multisession models (pooling data across five sessions over a decade) helped compensate for smaller sample sizes in certain sessions, still allowing for meaningful density trend assessments (Karanth and Nichols, 2017; Royle et al., 2014; Efford, 2025a). The low number of detections, recaptures, and individuals in our analyses likely impacted the precision of the population density estimates. Palmero et al. (2023a) emphasise that small sample sizes can increase variability in SCR models, potentially leading to biases or imprecise estimates.

In our study, the CV for the density estimates of the trend (D~**Session**) model excluding unsuitable habitat ranged from 20.9 % to 35.3 % for the left flank dataset and from 19.7 % to 34.3 % for the right flank dataset. According to Dormann (2017), a CV < 20 % indicates high precision, while CVs between 20 % and 30 % indicate moderate precision with acceptable results. Most of our estimates fell within the moderate precision range, though the higher CVs (>30 %) observed in the later years reflect increasing uncertainty as detections became sparser.

To mitigate these issues and improve the precision of density estimates, in future deterministic sessions we will try to make the following adjustments: increase the density of camera trap sites, utilize marking sites for camera-trap placement (Fležar et al., 2023; Krofel et al., 2025), extend the study durations beyond 60 days, expand the study area, as done for the 2023 session, to, hopefully, capture more individuals and obtain a higher number of (spatial) recaptures (Palmero et al., 2023a). In addition, conducting opportunistic camera trapping along trails and at marking sites before the start of the deterministic session could increase the probability of obtaining photographs from both flanks of individual lynx. This would improve individual identification and potentially allow future analyses to be performed on a single dataset, without needing to separate left and right flank images. If marking sites are used more systematically for camera placement, it will also be important to include site type as a covariate for detection probability in the SCR models, as it may influence detection rates (Fležar et al., 2025). Despite these limitations, the observed decline in lynx densities is still supported by the data, though there is some uncertainty in the exact magnitude of change. Lastly, the absence of sex-based information in our models represents another limitation. Sex differences may influence lynx movement and detection probability, as males and females often exhibit distinct movement patterns and territorial behaviours (Palmero et al., 2021; Vogt et al., 2014). For instance, males generally have larger home ranges and higher movement rates, which can lead to differential detectability and impact density estimates (Gerber et al., 2012; Mohamed et al., 2019; Vogt et al., 2014). Not accounting for such sex-based heterogeneity may result in biases and underestimated density estimations (Mohamed et al., 2019). Efford and Mowat (2014) highlighted that unmodeled heterogeneity, such as sex-specific detection and movement parameters, can reduce the precision of density estimates in SCR models, and may affect the accuracy when compensatory effects are insufficient (e.g., if one sex dominating detections due to differing movement or detection probabilities).

4.3. Conservation and management implications

Despite being highly threatened, lynx densities in the core area of the Balkan lynx fall within the range observed in other European populations, highlighting that this top predator typically exists at low densities across its range.

Using SCR models, lynx population densities have been assessed across several regions in Europe. Studies that included the whole habitat, without excluding unsuitable areas, reported densities ranging from 0.24 to 0.91 individuals per 100 km^2 in the French Jura Mountains (Gimenez et al., 2019), and from 0.69 to 1.33 individuals per 100 km^2 in the Bohemian Forest Ecosystem (Palmero et al., 2021). Palmero et al. (2023b) estimated 0.45 and 1.46 individuals per 100 km^2 in the Ukrainian-Belorussian border of Polesia and Chernobyl region, respectively and 0.46 individuals/100 km^2 in the Ukrainian Carpathians. Studies that kept only suitable habitat in their analyses also reported comparable results, with lynx densities in the Carpathian Mountains ranging from 0.26 to 1.85 individuals per 100 km^2 of suitable habitat in the Western Carpathians (Duľa et al., 2021), 0.58 and 0.81 individuals per 100 km^2 of suitable habitat in two areas of the Slovak Carpathians (Kubala et al., 2019) and 1.60–1.70 individuals per 100 km^2 of suitable habitat in the Romanian Carpathians (Iosif et al., 2022). The geographically closest population to the Balkan lynx and perhaps the most relevant in terms of future merging into a metapopulation is the Dinaric lynx population. Recent reinforcements in the Dinaric Mountains have raised densities from 0.83 to about 1.31 lynx/100 km^2 in Slovenia and 1.27 lynx/100 km^2 across the entire transboundary region (Fležar et al., 2025; Krofel et al., 2024). This growth (over 100 % in Slovenia) underscores the potential benefits of genetic and demographic reinforcement, which may serve as a valuable model for the Balkan lynx. Zimmermann and Foresti (2016) provided density estimates for the Swiss Alps, considering both the entire habitat and suitable habitat only, with estimates of 1.11 individuals per 100 km^2 when considering the whole habitat and 1.38 individuals per 100 km^2 when considering suitable habitat only. Exceptional density estimates were reported in Turkey, where Mengüllüoğlu et al. (2021) estimated an impressive density of 4.9 lynx per 100 km^2 of suitable habitat in Anatolia and Avgan et al. (2014) estimated a density of 4.20 independent lynx per 100 km^2 of suitable habitat or 3.17 independent lynx per 100 km^2 when all habitats were considered in the Ciglikara Nature Reserve. It is important to highlight that the Anatolian lynx population is quite different from most European lynx populations, including the Balkan lynx, as they do not rely predominantly on medium-sized ungulates. Instead, they feed heavily on abundant smaller prey, chiefly hares (Mengüllüoglu et al.,λ 2018, Melovski et al., 2022). Consequently, one should be cautious when comparing Anatolian lynx estimates to the Balkan or other European populations, given their contrasting resource use and habitat structure.

Despite having comparable population densities with other European populations, the Balkan lynx population has experienced a continuous decline, as observed through a decade-long camera-trap monitoring in its core area, Mavrovo NP as well as Munella Mt. in Albania (Hoxha et al., 2021). The observed population decline in its prime habitat cannot be attributed to technical (i.e. loss of trap nights) or improper sampling design but is likely driven by factors such as habitat disturbance, reduced prey availability, poaching, and genetic challenges associated with a small, inbred population. It is further fuelled by severe recent inbreeding and a very high mutational load, which could lead to inbreeding depression and reduced fitness (Gonev, 2025). Urgent actions are needed through the Balkan Lynx Recovery Programme (Melovski et al., 2021) to address not only conventional threats but also to enhance genetic diversity and mitigate inbreeding effects. It is of utmost importance to keep monitoring the core of the population and surroundings using the same rate (every two to three years) in order to follow the density, abundance and demography of the Balkan lynx. These findings will inform the development of targeted conservation strategies and contribute to evaluations for the IUCN Red List of Threatened Species and the Green Status of Species assessment, both essential steps for long-term recovery and conservation of the Balkan lynx. Long-term monitoring is crucial to track the population's status and demographic parameters, evaluate the effectiveness of recovery efforts, and ensure the survival of this critically endangered species. Given the proof of population decline in its prime area and genetic impairment, we recommend continuous monitoring and urgent reinforcement actions to halt further decline and enhance genetic diversity. Alongside any future release or reinforcement measures, we advocate a robust monitoring strategy that includes both camera-trapping and non-invasive genetics. Such a 'dual approach' has proven successful in other lynx populations, for example in the Dinaric region (Krofel et al., 2024), by confirming new litters, identifying immigrant or reintroduced animals, and gauging genetic diversity. Considering the high inbreeding levels (Gonev, 2025), genetic data collected in parallel with photographic detections would help track whether reinforcement efforts are curbing inbreeding, fostering population growth and secure the long-term viability of the population.

Ethics

Not applicable: This manuscript does not include human or animal research.

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Ethical statement

Data collection and fieldwork were carried out after obtaining research permission from the Ministry of Environment and Physical Planning of the Republic of North Macedonia (Permits number: 11–2186/2; 11–546/2; 11–1006/10, 11/1–1417/2019, 11/1–59/2023).

Declaration of Generative AI and AI-assisted technologies in the writing process

The AI tool [ChatGPT, version: GPT-4, OpenAI] was used to improve the formulation and clarity of some English sentences in this manuscript.

Declaration of Competing Interest

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

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Authors contribution

FZ, DM, AS, GI, IM conceptualized and designed the study. DM, AS, GI, AP, AG, VA, YH collected the data. IM analyzed the data. IM and DM wrote the manuscript. All co-authors read and provided useful contributions to the manuscript.

Data statement

The Balkan lynx is a critically endangered subspecies facing significant conservation challenges. Interactions with human activities pose serious threats, including poaching and other anthropogenic pressures. Providing accurate information on lynx locations can be detrimental for this subspecies, therefore the original data could not be shared.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03615.

Data availability

The data that has been used is confidential.

References

Avgan, B., Zimmermann, F., Güntert, M., Arıkan, F., Breitenmoser, U., 2014. The first density estimation of an isolated Eurasian lynx population in southwest Asia. Wildl. Biol. 20 (4), 217–221. https://doi.org/10.2981/wlb.00025.

Blanc, L., Marboutin, E., Gatti, S., Gimenez, O., 2013. Abundance of rare and elusive species: Empirical investigation of closed versus spatially explicit capture–recapture models with lynx as a case study. J. Wildl. Manag. 77 (2), 372–378. https://doi.org/10.1002/jwmg.453.

Bonn Lynx Expert Group (2021). Recommendations for the conservation of the Eurasian lynx in Western and Central Europe. Conclusions from the workshop of the "Bonn Lynx Expert Group" in Bonn, Germany, 16–19 June 2019. Cat News Special Issue 14. 78-86 pp. https://www.catsg.org.

Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Capt, S., Laass, J., Siegenthaler, A., & Breitenmoser, U., 2001. Koordinierte Forschungsprojekte zur Erhaltung und zum Management der Raubtiere in der Schweiz. Coordinated research projects for the conservation and management of carnivores in Switzerland. Projets de recherches coordonnés pour la conservation et la gestion des carnivores en Suisse.

Breitenmoser-Würsten, C., Breitenmoser, U., 2001. The Balkan lynx population – History, recent knowledge on its status and conservation needs. KORA Rep. Nr 7, 39.

Choo, Y.R., Kudavidanage, E.P., Amarasinghe, T.R., Nimalrathna, T., Chua, M.A.H., Webb, E.L., 2020. Best practices for reporting individual identification using camera trap photographs. Glob. Ecol. Conserv. 24, 01294. https://doi.org/10.1016/j.gecco.2020.e01294.

Dormann, C.F., 2017. Parametrische Statistik. Springer Berlin Heidelberg, Berlin, Heidelberg, Germany.

Dul'a, M., Bojda, M., Chabanne, D.B.H., et al., 2021. Multi-seasonal systematic camera-trapping reveals fluctuating densities and high turnover rates of Carpathian lynx on the western edge of its native range. Sci. Rep. 11, 9236. https://doi.org/10.1038/s41598-021-88348-8.

Efford, M., 2022. *An introduction to model specification in secr*.

Efford, M., 2025a. *Multi-session models in secr 5.2*.

Efford, M., Dawson, D., Robbins, C., 2004. DENSITY: Software for analysing capture-recapture data from passive detector arrays. Anim. Biodivers. Conserv. 27. https://doi.org/10.32800/abc.2004.27.0217.

Efford, M.G., Fewster, R., 2013. Estimating population size by spatially explicit capture-recapture. Oikos 122, 918–928. https://doi.org/10.2307/41937741.

Efford, M.G., Mowat, G., 2014. Compensatory heterogeneity in spatially explicit capture–recapture data. Ecology 95 (5), 1341–1348. https://doi.org/10.1890/13-1497.1.

Efford, M.G., Borchers, D.L., Byrom, A.E., 2009. Density Estimation by Spatially Explicit Capture–Recapture: Likelihood-Based Methods. In: Thomson, D.L., Cooch, E. G., Conroy, M.J. (Eds.), Modeling Demographic Processes In Marked Populations. Environmental and Ecological Statistics, 3. Springer, Boston, MA. https://doi.org/10.1007/978-0-387-78151-8_11.

Efford, M., 2025b. *secr: Spatially explicit capture-recapture models. R package version 5.2.0*.

Filipovski, G.J., Rizovski, R., Ristevski, P., 1996. The characteristics of the climate-vegetation-soil zones (regions) in the Republic of Macedonia. Makedonska akademija na naukite i umetnostite, Skopje, 1996 [in Macedonian].

Fležar, U., Aronsson, M., Černe, R., Pičulin, A., Bartol, M., Stergar, M., Rot, A., Hočevar, L., Topličanec, I., Sindičić, M., Gomerčić, T., Slijepčević, V., Krofel, M., 2023. Using heterogeneous camera-trapping sites to obtain the first density estimates for the transboundary Eurasian lynx (*Lynx lynx*) population in the Dinaric Mountains. Biodivers. Conserv. 32 (10), 3199–3216. https://doi.org/10.1007/s10531-023-02646-3.

Fležar, U., Krofel, M., Bartol, M., Černe, R., Hočevar, L., Trajbarič, A., Hvala, T., Prostor, M., Stergar, M., Aronsson, M., 2025. Hunter-engaged monitoring of the Eurasian lynx during the reinforcement process. Wildl. Biol., e01399 https://doi.org/10.1002/wlb3.01399.

Gardner, B., Reppucci, J., Lucherini, M., Royle, J.A., 2010. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. Ecology 91, 3376–3383. https://doi.org/10.1890/09-0804.1.

Gerber, B., Karpanty, S., Kelly, M., 2012. Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Popul. Ecol. 54, 43–54. https://doi.org/10.1007/s10144-011-0276-3.

Gimenez, O., Gatti, S., Duchamp, C., Germain, E., Laurent, A., Zimmermann, F., Marboutin, E., 2019. Spatial density estimates of Eurasian lynx (*Lynx lynx*) in the French Jura and Vosges Mountains. Ecol. Evol. 9, 11707–11715. https://doi.org/10.1002/ece3.5668.

Gonev, A., 2025. Quantifying the genetic load and recent inbreeding levels of the critically endangered Balkan lynx (*Lynx lynx balcanicus*). [Master's Thesis, Uppsala University].

Greenspan, E., Anile, S., Nielsen, C.K., 2020. Density of wild felids in Sonora, Mexico: a comparison of spatially explicit capture-recapture methods. Eur. J. Wildl. Res. 66, 60. https://doi.org/10.1007/s10344-020-01401-1.

Heurich, M., Schultze-Naumburg, J., Piacenza, N., Magg, N., Červený, J., Engleder, T., Herdtfelder, M., Sladova, M., Kramer-Schadt, S., 2018. Illegal hunting as a major driver of the source-sink dynamics of a reintroduced Lynx population in Central Europe. Biol. Conserv. 224, 355–365. https://doi.org/10.1016/j.biocon.2018.05.011.

Hoxha, B., Trajçe, A., Shyti, I., Lama, O., 2021. Results of the Balkan Lynx Extensive Camera trapping Survey – Winter/ Spring 2021, Albania. PPNEA Technical report, 20 pp.

Iosif, R., Popescu, V.D., Ungureanu, L., Şerban, C., Dyck, M.A., Promberger-Fürpass, B., 2022. Eurasian lynx density and habitat use in one of Europe's strongholds, the Romanian Carpathians. J. Mammal. 103 (2), 415–424. https://doi.org/10.1093/jmammal/gyab157.

Ivanov, Gj, Melovski, D., Janevski, R., Stojanov, A., Avukatov, V., Pavlov, A., 2018. Detecting alternative prey of the Balkan lynx using scat analysis. For. Rev. 49 (1), 06–13.

Kaczensky, P., Ranc, N., Hatlauf, J., Payne, J.C. et al. 2024. Large carnivore distribution maps and population updates 2017 – 2022/23. Report to the European Commission under contract N°09.0201/2023/907799/SER/ENV.D.3 "Support for Coexistence with Large Carnivores", "B.4 Update of the distribution maps". IUCN/SSC Large Carnivore Initiative for Europe (LCIE) and Istituto di Ecologia Applicata (IEA).

Kalle, R., Ramesh, T., Qureshi, Q., Sankar, K., 2011. Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture–recapture sampling. Acta Theriol. 56 (4), 335–342. https://doi.org/10.1007/s13364-011-0038-9.

Karanth, K.U., Nichols, J.D., 2017. Methods For Monitoring Tiger And Prey Populations. Springer Singapore. https://doi.org/10.1007/978-981-10-5436-5.

Krofel, M., Hočevar, L., Allen, M.L., 2017. Does human infrastructure shape scent marking in a solitary felid? Mamm. Biol. 87, 36–39. https://doi.org/10.1016/j.mambio.2017.05.003.

Krofel, M., U. Fležar, R. Černe, et al. 2024. Saving the Dinaric Lynx: Multidisciplinary Monitoring and Stakeholder Engagement Support Large Carnivore Restoration in Human-Dominated Landscape. bioRxiv. 2024.2010.2015.617164.

Krofel, M., Oliveira, T., Rovero, F., et al., 2025. Communication behavior of the snow leopard (*Panthera uncia*): understanding marking-behavior patterns to optimize camera-trapping studies. Behav. Ecol. Socio 79, 32. https://doi.org/10.1007/s00265-025-03574-8.

Kubala, J., Smolko, P., Zimmermann, F., Rigg, R., Tám, B., Iľko, T., Foresti, D., Breitenmoser-Würsten, C., Kropil, R., Breitenmoser, U., 2019. Robust monitoring of the Eurasian lynx *Lynx lynx* in the Slovak Carpathians reveals lower numbers than officially reported. Oryx 53 (3), 548–556. https://doi.org/10.1017/S003060531700076X.

Marrotte, R.R., Howe, E.J., Beauclerc, K.B., Potter, D., Northrup, J.M., 2022. Explaining detection heterogeneity with finite mixture and non-Euclidean movement in spatially explicit capture-recapture models. PeerJ 10, e13490. https://doi.org/10.7717/peerj.13490.

Melovski, D., Ivanov, Gj, Stojanov, A., Trajçe, A., Zimmermann, F., von Arx, M. 2008. First camera-trap survey in the National Park Mavrovo, Macedonia. In Proceedings of the International Conference on Biological and Environmental Sciences, Republic of Albania, FNS pp. 312–315. PPNEA, Tirana.

Melovski, D., Breitenmoser, U., von Arx, M., Breitenmoser-Würsten, C., Lanz, T., 2015. *Lynx lynx ssp. balcanicus* (errata version published in 2016). The IUCN Red List of Threatened Species 2015: Downloaded on 03 August 2024.

Melovski, D., von Arx, M., Avukatov, V., Breitenmoser-Würsten, C., Đurović, M., Elezi, R., Gimenez, O., Hoxha, B., Hristovski, S., Ivanov, G., Karamanlidis, A.A., Lanz, T., Mersini, K., Perović, A., Ramadani, A., Sanaja, B., Sanaja, P., Schwaderer, G., Spangenberg, A., Stojanov, A., Trajçe, A., Breitenmoser, U., 2018. Using questionnaire surveys and occupancy modelling to identify conservation priorities for the Critically Endangered Balkan lynx *Lynx lynx balcanicus*. Oryx 54 (5), 706–714. https://doi.org/10.1017/S0030605318000492.

Melovski, D., Ivanov, G., Stojanov, A., Avukatov, V., Gonev, A., Pavlov, A., Breitenmoser, U., von Arx, M., Filla, M., Krofel, M., Signer, J., Balkenhol, N., 2020. First insight into the spatial and foraging ecology of the critically endangered Balkan lynx (*Lynx lynx balcanicus*, Buresh 1941). Hystrix, Ital. J. Mammal. 31 (1), 26–34. https://doi.org/10.4404/hystrix-00254-2019.

Melovski, D., Trajçe, A., Von Arx, M., Stojanov, A., Hoxha, B., Pavlov, A., Brix, M., Schwaderer, G., Spangenberg, A., Shyti, I., Lama, O., Avukatov, V., Koçi, Ivanov, Gj, Xherri, Xh, Sanaja, B., Breitenmoser-Würsten, Ch, Breitenmoser, U., 2021. Balkan lynx and the Balkan Lynx Recovery Programme. Cat News, Special Issue 14, pp 16-18.

Melovski, D., Krofel, M., Avukatov, V., Fležar, U., Gonev, A., Hočevar, L., Ivanov, G., Leschinski, L., Pavlov, A., Stojanov, A., Veapi, E., Mengüllüoğlu, D., 2022. Diverging ecological traits between the Balkan lynx and neighbouring populations as a basis for planning its genetic rescue. Mamm. Biol. 102 (5–6), 1697–1708.

Mengüllüoglu, D., Ambarlı, H., Berger, A., Hofer, H., 2018. Foraging ecology of Eurasian lynx populations in southwest Asia: conservation implications for a diet specialist. Ecol. Evol. 8 (18), 1–13.

Mengüllüoğlu, D., Edwards, S., Hofer, H., Berger, A., 2021. Female and male Eurasian lynx have distinct spatial tactics at different life-history stages in a high-density population. Ecol. Evol. 11, 10432–10445. https://doi.org/10.1002/ece3.7846.

Mohamed, A., Sollmann, R., Wong, S., Niedballa, J., Abrams, J., Kissing, J., Wilting, A., 2019. Counting Sunda clouded leopards with confidence: Incorporating individual heterogeneity in density estimates. Oryx 55, 1–10. https://doi.org/10.1017/S0030605318001503.

Obbard, M.E., Howe, E.J., Kyle, C.J., 2010. Empirical comparison of density estimators for large carnivores. J. Appl. Ecol. 47 (1), 76–84. https://doi.org/10.1111/j.1365-2664.2009.01758.x.

Palmero, S., Belotti, E., Bufka, L., Gahbauer, M., Heibl, C., Premier, J., Weingarth-Dachs, K., Heurich, M., 2021. Demography of a Eurasian lynx (*Lynx lynx*) population within a strictly protected area in Central Europe. Sci. Rep. 11, 19868. https://doi.org/10.1038/s41598-021-99337-2.

Palmero, S., Smith, A.F., Kudrenko, S., Gahbauer, M., Dachs, D., Weingarth-Dachs, K., Kashpei, I., Shamovich, D., Vyshnevskiy, D., Borsuk, O., Korepanova, K., Bashta, A.-T., Zhuravchak, R., Fenchuk, V., Heurich, M., 2023b. Shining a light on elusive lynx: Density estimation of three Eurasian lynx populations in Ukraine and Belarus. Ecol. Evol. 13, e10688. https://doi.org/10.1002/ece3.10688.

Palmero, S., Premier, J., Kramer-Schadt, S., Monterroso, P., Heurich, M., 2023a. Sampling variables and their thresholds for the precise estimation of wild felid population density with camera traps and spatial capture–recapture methods. Mammal. Rev. 53 (4), 223–237. https://doi.org/10.1111/mam.12320.

Pesenti, E., Zimmermann, F., 2013. Density estimations of the Eurasian lynx (*Lynx lynx*) in the Swiss Alps. J. Mammal. 94 (1), 73–81.

R Core Team, 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rovero, F., Zimmermann, F., 2016. Camera features related to specific ecological applications. Camera Trapping for Wildlife Research. Pellagic Publishing, pp. 8–18.

Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B., 2014. Spatial Capture-Recapture. Elsevier Science. ⟨https://books.google.ch/books?id=RO08-S-amZMC⟩.

Sollmann, R., 2018. A gentle introduction to camera-trap data analysis. Afr. J. Ecol. 56, 740–749. https://doi.org/10.1111/aje.12557.

Srivathsa, A., Parameshwaran, R., Sharma, S., Karanth, K.U., 2015. Estimating population sizes of leopard cats in the Western Ghats using camera surveys. J. Mammal. 96 (4), 742–750. https://doi.org/10.1093/jmammal/gyv079.

State statistical office of the Republic of Macedonia, 2022. Census 2021 - 115 pp., Skopje, North Macedonia.

Udevitz, M.S., Gould, W.R., 2014. Abundance: Population Size and Density Estimation. Wiley StatsRef: Statistics Reference Online. John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118445112.stat07650.

Vogt, K., Zimmermann, F., Kölliker, M., Breitenmoser, U., 2014. Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behav. Process. 106, 98–106. https://doi.org/10.1016/j.beproc.2014.04.017.

von Arx, M., Breitenmoser-Würsten, Ch, Zimmermann, F., Breitenmoser, U., 2004. Status and conservation of the Eurasian lynx (Lynx lynx) in Europe in 2001 (KORA Report No.19, pp. 1–330). KORA, Bern, Switzerland.

Weingarth, K., Zeppenfeld, T., Heibl, C., Heurich, M., Bufka, L., Daniszová, K., Müller, J., 2015. Hide and seek: Extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. Biodivers. Conserv. 24 (12), 2935–2952. https://doi.org/10.1007/s10531-015-0986-5.

Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and management of animal populations: Modeling, estimation, and decision making. Academic Press.

Zimmermann, F., Foresti, D., 2016. Capture-recapture methods for density estimation. In: Francesco Rovero, Zimmermann, F. (Eds.), Camera trapping for Wildlife Research. Pelagic Publishing, pp. 95–141.

Zimmermann, F., Breitenmoser-Wuersten, C., Molinari-Jobin, A., Breitenmoser, U., 2013. Optimizing the size of the area surveyed for monitoring a Eurasian lynx (*Lynx lynx*) population in the Swiss Alps by means of photographic capture-recapture. Integr. Zool. 8, 232–243.

Zimmermann, F., Kunz, F., Foresti, D., Asselain, M., Ravessoud, T., Schwehr, P. et al. (2015) Abondance et densité du lynx dans le Sud du Jura suisse: estimation par capture–recapture photographique dans le compartiment I durant l'hiver 2014/15. KORA Report No. 69. KORA, Bern, Switzerland.

Zimmermann, F., Kunz, F., Rhein, K., Shepherd, M., Tschanz, P., Breitenmoser-Würsten, C. & Breitenmoser, U. (2016) Abundanz und Dichte des Luchses in den Nordwestalpen: Fang-Wiederfang-Schätzung mittels Fotofallen im K-VI im Winter 2015/16. KORA Report No. 73. KORA, Bern, Switzerland.