Eurasian lynx density and habitat use in one of Europe's strongholds, the Romanian Carpathians

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The Eurasian lynx (*Lynx lynx*) faces population declines in the western part of its range, and its ecological requirements are poorly understood in the eastern part of its range. The Romanian Carpathians harbor an intact large carnivore community, in which lynx co-occur with bears (*Ursus arctos*), wolves (*Canis lupus*), and humans (*Homo sapiens*), with which they potentially compete for ungulate prey. We provide a science-based estimate of lynx density and habitat use, combining non-invasive monitoring techniques (camera trapping) with spatially explicit capture-recapture models (SECR) in the Southern Carpathians of Romania. We sampled 59 and 76 trap stations during two monitoring sessions (winter and autumn), identified at least 30 individuals, from which we reconstructed encounter histories for 23 individuals. SECR modeling resulted in similar density estimates between winter and autumn (1.6 ± 0.39 *SE* and 1.7 ± 0.38 *SE* lynx/100 km², respectively), but the cumulative number of lynx detected reached the asymptote faster during autumn, suggesting that monitoring prior to the mating season is preferable. Density varied within and across sessions with topography (slope), percent forest cover, and landscape heterogeneity (i.e., agricultural mosaic). Density hotspots shifted between low-altitude agricultural mosaic during winter and more rugged, mid-altitude forest stands during autumn. Estimated densities of lynx in the Romanian Carpathians are higher than those reported in the Alps or Slovak Carpathians, highlighting the importance of this population as a source both for natural recolonization and recent reintroduction programs. When used in an SECR framework, camera trapping is an efficient method for assessing spatial and temporal variation in lynx population density in the remote Romanian Carpathians. We recommend this methodology for improving lynx population estimates and to monitor lynx population trends nationwide.

Key words: abundance, camera trapping, density hotspot, detection, habitat use, *Lynx lynx*, spatially explicit capture recapture

Population viability of large carnivores varies across Europe based on the economic status (Kojola et al. 2018), management history (Salvatori et al. 2002), and public attitudes (Dressel et al. 2015), inherent to individual countries in the European Union (EU). The EU Habitats Directive legislation enabled the recolonization of former carnivore ranges in human-dominated landscapes (Chapron et al. 2014). Strict protection and conservation measures allowed apex predators such as wolves (*Canis lupus*) to recolonize large portions of their historical range by dispersing thousands of kilometers from core populations in southern Europe (Mulej et al. 2013). Trends in population recovery are less clear for cryptic species such as the Eurasian lynx (*Lynx lynx*) or European wildcat (*Felix sylvestris*), which lack data both on population trends at broad geographic scales, and basic ecological information on density and habitat use in core areas that can act as source of dispersers. For example, population viability of European wildcats in southern Spain is uncertain as habitat fragmentation continues to affect population connectivity (Gil-Sánchez et al. 2020). Iberian lynx (*Lynx pardinus*) also exhibits severe impediments to population recovery, highlighting an urgent need to protect lynx habitat outside reserves (Garrote et al. 2020). In sum, the capacity of felid populations to recover in portions of their historical ranges appear limited relative to that of other apex predators (Goana et al. 1998; Molinari-Jobin et al. 2010).

In 2000, the Eurasian lynx (hereafter "lynx") population was estimated at approx. 7,200 individuals across Europe, but methodological shortcomings and inconsistencies in field methods cast doubt on this estimate (Breitenmoser et al. 2000). Lynx face increasing pressure from habitat degradation, reduced prey availability, and high human-related mortality (Breitenmoser-Würsten et al. 2007). The species was extirpated from the Alps, Jura, and Dinaric Mountains during the 20th century; managers started reintroduction programs using individuals from Central and Eastern European populations (Linnell et al. 2009), yet success has been limited (Vandel et al. 2006; Mueller et al. 2020). Concomitantly, donor populations in Eastern Europe are lacking reliable density and demographic data (Rozylowicz et al. 2011; Popescu et al. 2016), such that removal of individuals, unsustainable hunting quotas of the prey base, and rapid deforestation, all may compromise population viability.

The Romanian Carpathians serve as a stronghold for carnivore populations in Europe (Kaczensky et al. 2012) and are characterized by a well-connected forest ecosystem interspersed with traditional agricultural landscapes with significant areas of natural vegetation. This mosaic provides habitat, food, and space requirements for a viable population of Eurasian lynx, as well as other large carnivores and their ungulate prey (Salvatori et al. 2002; Chapron et al. 2014). Despite their importance for carnivore conservation in Europe in general, the Romanian Carpathian populations are remarkably understudied (Promberger–Fürpass et al. 2002; Rozylowicz et al. 2010); there is no science-based monitoring at a scale relevant to carnivores' spatial ecology, and lynx have the least data available for informing conservation (Popescu et al. 2016).

Determining a baseline population size is a prerequisite for evaluating the long-term population viability of lynx in Romania, and for developing a robust population monitoring program (Breitenmoser et al. 2000). Because physical capture and recapture of animals is time and cost intensive, and induces stress in captured animals, camera trapping has emerged as an effective non-invasive sampling method to identify individuals based on unique marks (spots, stripes, scars). These data can be used to estimate animal density in a spatially explicit capture-recapture (SECR) framework (Borchers and Efford 2008; Royle et al. 2014), and the method is suitable for European lynx (Zimmermann et al. 2013). SECR incorporates the natural spatial variation in animal movement (activity centers; Boyce and McDonald 1999), and provides robust density estimates without biased assumptions around calculating the effective sampling area (Foster and Harmsen 2012; Gilbert et al. 2021).

We aimed to demonstrate the feasibility of camera trapping as a monitoring tool for Eurasian lynx in the Romanian Carpathians, using SECR models to estimate density and abundance during two distinct seasons. We also modeled density as a function of various spatial predictors and evaluated seasonal variation of density patterns, thus effectively linking density to resource selection. Specifically, our objectives were: (1) to compare density estimates for lynx across two distinct seasons, autumn and winter; and (2) to evaluate environmental and human-disturbance factors driving potential shifts in spatial density patterns between the two sampling sessions. We hypothesized that autumn monitoring would provide more robust population estimates compared to winter monitoring (which includes the full mating season), because the autumn home ranges are more stable, thereby increasing the detection probability and recapture rate (Weingarth et al. 2015). Our preliminary observations and other studies focused on habitat selection (Filla et al. 2017) suggested that lynx occupancy shifts between different habitats, with the agricultural mosaic being selected during winter, likely because it attracts roe deer (*Capreolus capreolus*) due to lower snow cover. We believe that our study has the potential to inform the conservation and management of lynx across Romania by providing insights into population ecology and viability, and setting a baseline for a national monitoring program. In addition, our work may have strong ramifications across Europe by providing a direct comparison with other viable European lynx populations, and by providing valuable information on the donor lynx population for future reintroductions.

Materials and Methods

Study area.—The 1,200 km² study area is located in the Romanian Southern Carpathians, ranging in altitude between 600 and 2,400 m (Fig. 1). The area includes a national park and overlaps with four Sites of Community Importance that form part of the Natura 2000 network, the European network of protected areas. Deciduous, coniferous, and mixed forests in equal proportions cover 62% of the area. Livestock grazing is common in the alpine areas, whereas lowlands are characterized by small scale subsistence farming and traditionally maintained landscapes (mosaics of pastures, hayfields, and forests) as well as some tourism. In the last three decades, the area was affected by forest clear-cut operations (Kuemmerle et al. 2009) and logging still is the most important economic activity. The study area harbors an intact mammal assemblage, including large and meso-carnivores (brown bear; wolf; wildcat; fox, *Vulpes vulpes*; and badger, *Meles meles*) and their prey (roe deer; red deer, *Cervus elaphus*; chamois *Rupicapra rupicapra*; wild boar *Sus scrofa*; and leporids, e.g., hare, *Lepus europaeus*).

Monitoring sessions and camera trapping.—We carried out camera trapping across two monitoring sessions: (1) 17 December 2018 to 31 March 2019 (105 days; hereafter called "winter" session), and (2) 9 October 2019 to 16 January 2020 (100 days; although this session includes early winter as well, for simplicity we hereafter call it the "autumn" session). Demographic closure in camera trapping was addressed in relatively short, up to 3-month sessions for lynx (Kubala et al. 2019), but requires longer sessions for more elusive felids like the European wildcat (up to 3 years monitoring in Sicily; Anile et al. 2014) or ocelot (*Leopardus pardalis*, in the dense Atlantic Forest; Di Bitetti et al. 2006). The length and timing of our monitoring sessions were based on the study by Weingarth et al. (2015), who suggested that 80–120 days were necessary to obtain sufficient recaptures at camera traps and an optimal time window for monitoring between September and November.
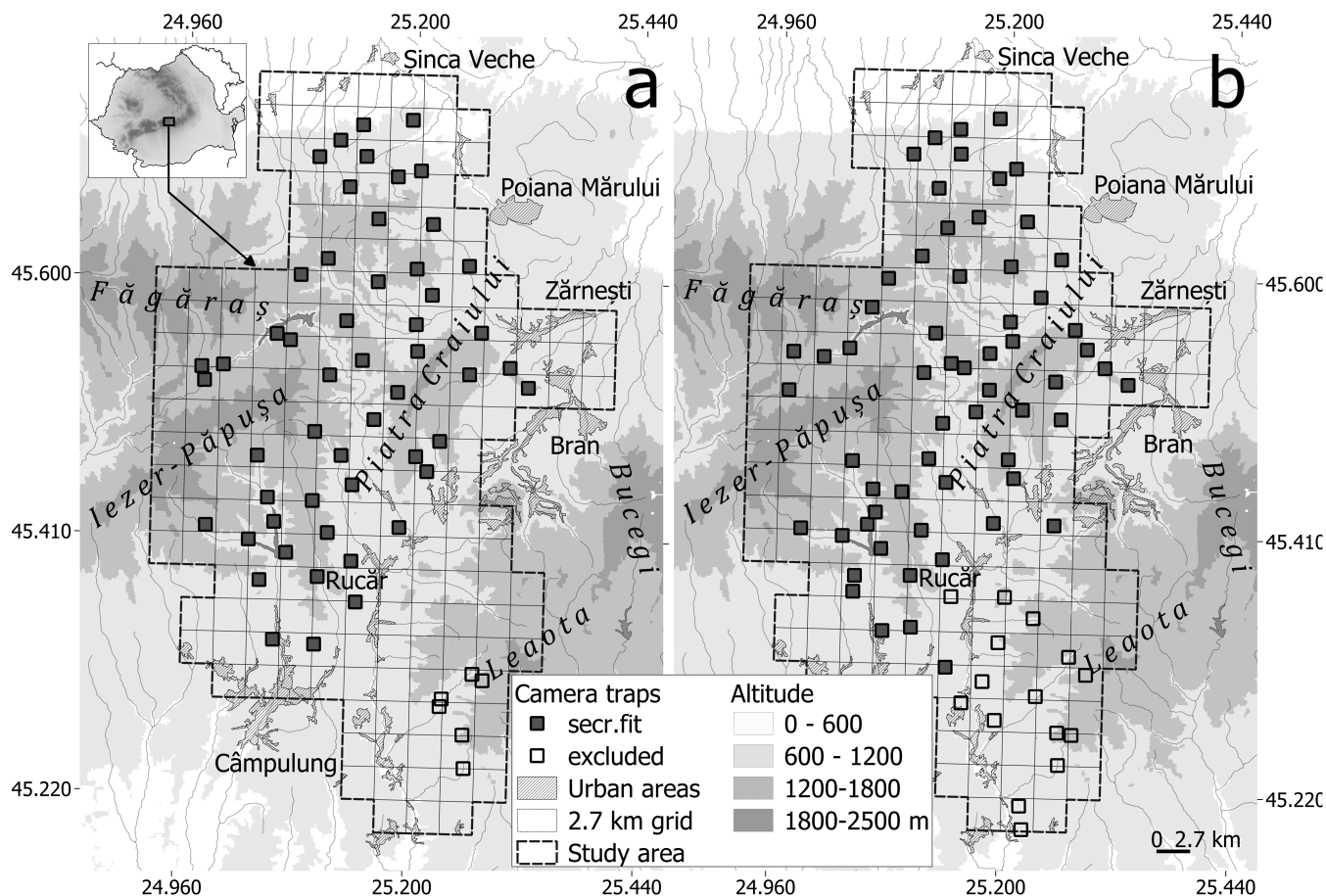
Fig. 1.—Study area for camera trapping of Eurasian lynx in the Southern Carpathians, Romania. Panel (a) represents the winter session with 59 traps functioning between 17 December 2018 and 31 March 2019. Panel (b) represents the autumn session with 76 traps functioning between 9 October 2019 and 15 January 2020. Note that the majority of traps overlap from one session to another and symbology varies between traps, one for traps used for fitting spatially explicit capture recapture models, and one for traps excluded from modeling due to insufficient data.
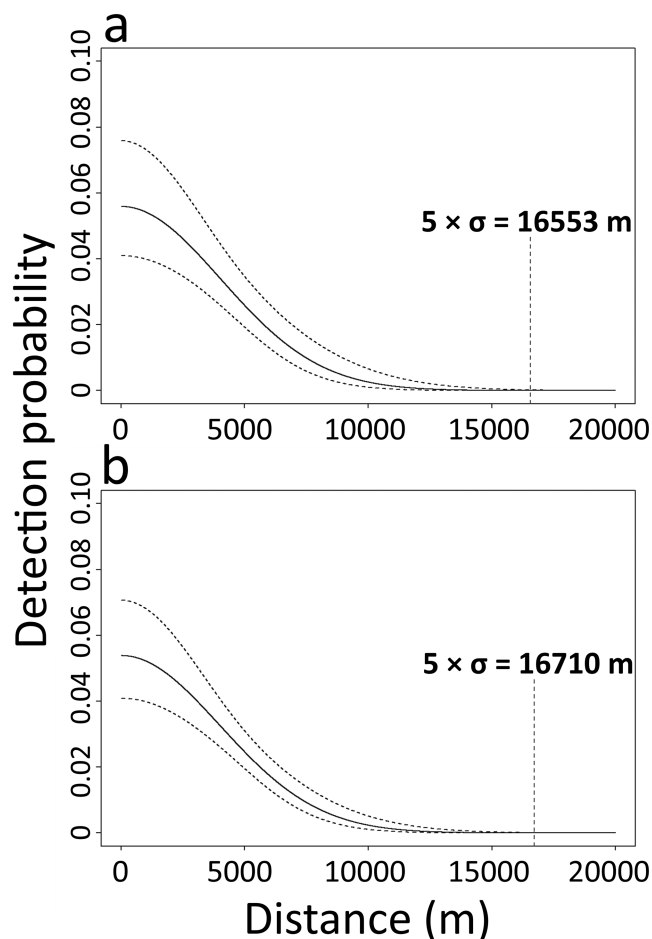
Similar to Pesenti and Zimmerman (2013), we first divided our study area into a grid of 2.7 × 2.7 km cells and removed cells with more than ⅔ of their area exceeding 1,800 m altitude (above the tree line) and cells more than 1/2 of their area covered by urban landscape features. From the remaining area, we sampled every other cell; when it was not possible to access a selected cell, we used an adjacent cell. We installed 59 camera trap stations during winter, and 76 camera trap stations during autumn, with high spatial overlap between seasons (Fig. 1). Each trap station had two cameras installed at a height of 40–60 cm opposite from each other and pointing towards the expected animal paths in an almost rectangular angle, to obtain the best images of the flanks of lynx. We used white flash cameras (Cuddeback C1 Model 1279, Cuddeback, Green Bay, Wisconsin) and Bushnell Trophy Cam infrared camera (Bushnell, Overland Park, Kansas). We installed the camera traps predominantly on animal trails along mountain ridges, or, where snow cover limited accessibility, on logging and unpaved forestry roads. We checked trap stations every two weeks. When new logging operations were likely to reduce detection probability or affect the cameras themselves, we moved the cameras within the same grid cell.

Lynx identification and encounter histories.—Lynx were identified based on the size and shape of spots or rosettes on their coat and their relative position to each other (Thüler 2002). Determining the sex of lynx from lateral images was limited to females with their kittens and, occasionally, when the genital area was clearly visible, on photographs of the dorsal area. We built encounter histories for each individual, pooling each 5 consecutive days to one sampling occasion (O'Connell et al. 2010). We used the identified kittens and family groups to reconstruct the encounter histories of the females. Because reloading the white flash cameras takes time, it is hard to always capture all individuals of a family group. Thus, we equated the presence of a kitten as the presence of the respective female. While we used all the camera traps to describe lynx detections, for the purpose of SECR analysis, we removed encounter histories from 7 camera traps for the winter session, and 15 for the autumn session (Fig. 1). These cameras were located in a disjunct region and had a weak encounter history data. Furthermore, they largely returned poor quality pictures that did not allow individual identification. Pooled across both sessions, 63.6% of the lynx picture events obtained there allowed identification compared to 79.2% in the rest of the study area.

During the autumn however, only 16.7% of the lynx picture events obtained from these cameras allowed identification of individuals. Density estimates are affected by the size of the effective sampling area, which in SECR includes a buffer around the sampling grid (see below). Expanding the effective sampling area by including an area with low identifiability of individuals would bias the overall density estimates, as well as alter the relationships between density and environmental predictors; removing the cameras therefore eliminated such a bias and strengthened the inference.

Lynx detection and abundance modeling.—To model detection, we calculated the sigma (σ) model parameter using a root pooled spatial variance function (Calhoun and Casby 1958; Slade and Swihart 1983) as a measure of the 2D dispersion of the locations where individuals were detected, pooled over individuals (Efford 2020). We selected a buffer width of 5 × σ around our detectors to calculate the effective sampling area (Borchers and Efford 2008), because the probability of capturing a lynx from outside of this buffer converged to zero (Fig. 2; Supplementary Data SD1; see also Rovero and Zimmermann 2016). The value of σ was 3,310 m in winter and 3,343 m in autumn. We used the half-normal function (Efford 2020) for all analyses (Supplementary Data SD1). Finally, we used 4 automatic predictors to model detection parameters (*b*, permanent global learned response; *bk*, permanent detector-specific learned response; *t*, time factor (one level for each occasion), and *T*, time trend (Efford 2020); and a *null* model. We then compared model performance using AIC (Akaike 1973). The argument *bk* detection parameter performed best (Supplementary Data SD1); we therefore used it to fit all SECR models.

We removed low suitability cells with mostly urban landscape using a habitat/nonhabitat mask at a 1 × 1 km resolution. Nonhabitat was calculated as cells with proportional cover of human dominated landscape >0.7 and proportion of forest <0.1, based on Corine Land Cover (CLC) 2018 (European Environment Agency 2020). These thresholds are based on our direct observations of occurrence patterns and similar studies (Basille et al. 2009; Filla et al. 2017; Supplementary Data SD1). After several model iterations, the final SECR model contained an observation model accounting for variable effort across the 5-day sampling windows and the habitat/non-habitat mask (Supplementary Data SD2).

Predictors of lynx density.—To predict variation in lynx density across the study area, we fitted SECR state (observation) models against environmental predictors using a spatial Poisson process for animal activity centers (Borchers and Efford 2008; Efford 2020). The density predictors used were: [Alt], mean altitude per cell in meters; [Slo], mean slope measured as degrees; [TRI9], a terrain roughness index averaged for nine neighboring cells; [PublicRoad] as average density of paved and unpaved roads; [OpenHab] % cover of open habitat; [AgriculturalMosaic] % cover of traditionally managed landscape; [CLC_311], [CLC_312], and [CLC_313] % cover of deciduous, coniferous, and mixed forest respectively, as extracted from CLC 2018. We defined [Forest] by merging all forest cover types; [OpenHab] by merging CLC classes 243, 321, 322, 332, 333, 411, and 512, classes that include habitats such alpine grasslands and bare rocks; [AgriculturalMosaic] by merging CLC classes 111, 112, 121, 142, 211, 222, 231, and 242, including crops, orchards, and pastures; and [Reclass] as the dominant habitat category per cell with five classes: deciduous, coniferous, mixed forest, and open habitat and human dominated landscape. We scaled all predictors prior to fitting the models, and we tested correlations between predictors. We did not include [Alt], [Slo], and [TRI9] in the same model because they were highly correlated (Pearson's $r > 0.7$).

The modeling framework and workflow uses package "secr" implemented in the R environment (Efford 2020) and is detailed in Supplementary Data SD1. We used QGIS (QGIS Development Team 2018) for all GIS processing of spatial data.

Fig. 2.—Detection probability with increasing distance from our trap array used to derive the effective sampling area for estimating lynx population size in a spatially explicit capture recapture approach. Panel (a) represents the winter session and panel (b) represents the autumn session. The vertical dashed line shows the 5 × σ buffer width where the probability of detecting lynx from outside of the sampling area converges to zero.

RESULTS

Lynx detections at cameras.—Camera trapping yielded 474 and 385 images of lynx for winter and autumn sessions, respectively,

which were merged into 148 and 153 distinct lynx detection events. Cameras monitored lynx activity for 5,916 effective trap nights in the winter session (95.5% of the sessions), and 7,216 effective trap nights in the autumn session (97.3% of the sessions). Lynx were detected at 71.2% of trap stations during winter, compared to 64.5% of the trap stations during autumn (Table 1).

Between the two sessions collectively, we identified a minimum of 30 different lynx, with 15 individuals identified as males and 6 as females (13 males and 5 males in winter; 9 males and 6 females in autumn). While across both sessions, 23 identified lynx remained constant, six animals identified during the winter were no longer recorded in autumn (four males and two of unknown sex), and four unknown sex lynx were identified for the first time during autumn (Supplementary Data SD3). Recapture rates were high during both sessions: 4.04 detections per individual in winter and 4.54 detections per individual in autumn, with a maximum of 16 detections per individual (Fig. 3; Supplementary Data SD4). We also observed females with kittens: four females with one or two kittens in winter for a total of six kittens, three females with two or three kittens in autumn, for a total of nine kittens.

The spatial pattern of lynx recaptures at camera stations was complex. Some individuals had only scattered recaptures on the map, others appear to have stable home ranges, and yet others appeared to shift home ranges between sessions (Supplementary Data SD4). Males had more recaptures per trap than females during the winter session (average pooled across identified males = 2.1 ± 0.27 recaptures, females = 1.3 ± 0.13 recaptures). During autumn, however, males and females had an equal number of recaptures per trap (1.6 ± 0.15 and 1.6 ± 0.16 recaptures, respectively; Fig. 3). Movements of males and females did not differ during the winter session ($U = 358.0$, $P = 0.204$), but males showed significantly longer movement than females during autumn ($U = 552.5$, $P = 0.021$; Supplementary Data SD5). Recaptures of the same individual occurred at camera trap stations that were up to 21.8 km from each other during the winter, and 15.0 km during the autumn (Supplementary Data SD5). The number of trap stations at which individuals were captured ranged between 1 and 8 (average pooled across all identified lynx = 3.68 ± 0.56 camera locations in autumn session), and we did not find significant differences in number camera traps with relocations between males and females ($U = 25.5$, $P = 0.674$ in winter; $U = 19.0$, $P = 0.379$ in autumn).

Lynx abundance and density.—The top SECR models for estimating regional abundance of lynx in our study area used all individuals pooled across sexes, and included the habitat mask for autumn, and no habitat mask for winter (but the top model was within 1 AICc unit from the second ranked model which included the habitat mask; Supplementary Data SD2). Based on the models with habitat mask, we estimated an abundance of 44.12 ± 8.48 adult lynx in winter, and 48.06 ± 8.11 in autumn (Table 2). These estimates do not include the number of kittens observed in each session.

After applying the $5 \times \sigma$ buffer around camera traps and the habitat mask in the SECR model, we obtained an effective sampling area of 2,729.5 km² for winter and 2,767.4 km² for autumn. Within these sampling areas, we estimated an average adult lynx density of 1.60 ± 0.39 *SE* and 1.73 ± 0.38 *SE* lynx/100 km², for winter and autumn, respectively (Table 2).

Predictors of lynx density.—For the winter session, multiple competing models predicted lynx density (Supplementary Data SD6); while the top predictor was [PublicRoad] (based on single-variable models), we did not include it in the final model for spatial predictions, because it likely is an outcome of placing cameras in accessible areas near roads during heavy snowpack winter conditions. Other predictors for density in this session were % cover of mixed forest [CLC313] and % cover of agricultural mosaic [AgriculturalMosaic]. For the autumn, [AgriculturalMosaic] and [Slo] were good predictors of density, along with % cover of coniferous forest [CLC312]. Thus, we used the following global model for projecting density spatially during both sessions, which included a quadratic term for slope: [Forest + AgriculturalMosaic + Slo + Slo²]. The resulting spatial models showed a shift in density hotspots (1.5 – 2 lynx/100 km²) from lower altitude, less steep landscapes (interface between forest, agriculture, and villages) during winter, to forest habitat at higher altitudes during autumn (Fig. 4).

DISCUSSION

We provide an assessment of Eurasian lynx density in one of Europe's strongholds for this species, the Romanian Carpathians, using camera trap data and SECR Lynx density was similar between the winter and the autumn sessions (1.6 ± 0.39 *SE* and 1.7 ± 0.38 *SE* adult lynx/100 km² respectively), but the cumulative number of detected lynx versus sampling occasions reached the asymptote faster during the autumn monitoring. This suggests that monitoring from early autumn through December/January, prior to the mating season, is preferable for the Romanian lynx population, corroborating the findings of Weingarth et al. (2015) in a Central-European

Table 1.—Information on trap stations functionality, success rates and image events for the Eurasian lynx in two monitoring sessions. *Images and encounters refer to the entire time span the trap stations were active, including the installation and dismounting periods (approximately 2 weeks before and after the period used for statistical evaluation).

| Session	Period	Days	Effective trap nights (%)	Success rate of traps* %	Lynx images*	Lynx encounters*	Identification rate %
Winter	12/17/2018–03/31/2019	105	5,916 (95.5)	71.2	474	148	81.1
Autumn	10/09/2019–01/16/2020	100	7,216 (97.3)	64.5	385	153	85.0

population. The densities estimated in our study area are higher than the ones reported in the Swiss Alps (1.04 – 1.42 lynx/ 100 km²; Zimmermann et al. 2013), and the Jura Mountains (0.7 – 0.8 lynx/100 km², Breitenmoser-Wursten et al. 2007; 0.24 – 0.91 lynx/100 km², Giménez et al. 2019). When compared with populations from the Slovak Carpathians, which have environmental conditions similar to our study area, our density estimates also were higher (i.e., 1.4 lynx/100 km², Smolko et al. 2018; and 0.5 lynx/100 km², Kubala et al. 2019). In addition, our observations on reproductive females suggest that litter size is two to three kittens, which is consistent with the average litter

size recorded in the Jura Mountains (Breitenmoser-Würsten et al. 2007).

There are several factors that may explain differences in lynx density between our study and that in other regions of Europe. First, lynx in our region likely experience low human-induced mortality rates, due to relatively lower levels of human impact. For example, we expect road mortality to be lower in the Romanian Carpathians due to a lower density of high-traffic roads, reduced access and anti-poaching enforcement. There are no highways in our study area, and only one high traffic national road passes through potentially suitable lynx habitat. In contrast, road mortality contributed to the decline of a reintroduced lynx population in the Jura Mountains (Breitenmoser-Würsten et al. 2007) and is the main cause of mortality for the Iberian lynx in southern Spain (Garrote et al. 2020). These findings corroborate studies in North America, which also suggest that felids are susceptible to roadkill, strongly affecting their population dynamics (e.g., cougars, *Puma concolor*, Dickson and Beier 2002; and bobcats, *Lynx rufus*, Nielsen and Woolf 2002; Bencin et al. 2019). In addition to mortality from vehicle strikes, human access to remote areas via snowmobiles during winter determined high levels of poaching in Scandinavian lynx populations (Andrén et al. 2006).

Second, our study area likely has a higher level of acceptance of lynx by the rural communities and livestock breeders in particular (Lescureux et al. 2011), and illegal killing likely is low and accidental. In contrast, Breitenmoser-Würsten et al. (2008) estimated illegal killing reached 32% in a radio-collared lynx population in the Jura Mountains due to a low level of acceptance from local and hunting communities. Iberian lynx populations also were impacted by high mortality from nonselective predator control programs (Gil-Sánchez and McCain 2011). In our area, both ungulate and predator populations benefited from the no-hunting policy of the CARPATHIA initiative, which together with Piatra Craiului National Park, resulted in a hunting-free zone of >80,000 ha, including effective anti-poaching enforcement.

The Romanian Carpathians seem to support higher lynx densities although the ungulate abundance in our study area is not as high as in Western Europe (Promberger–Fürpass et al. 2001). This could be explained by the availability of highly suitable habitat (large stands of old and mature forest), and by the high regional connectivity with compact forests juxtaposed to the agricultural mosaic that provide additional food resources. Habitat connectivity allows both lynx and their prey to migrate between forest and traditionally maintained landscapes
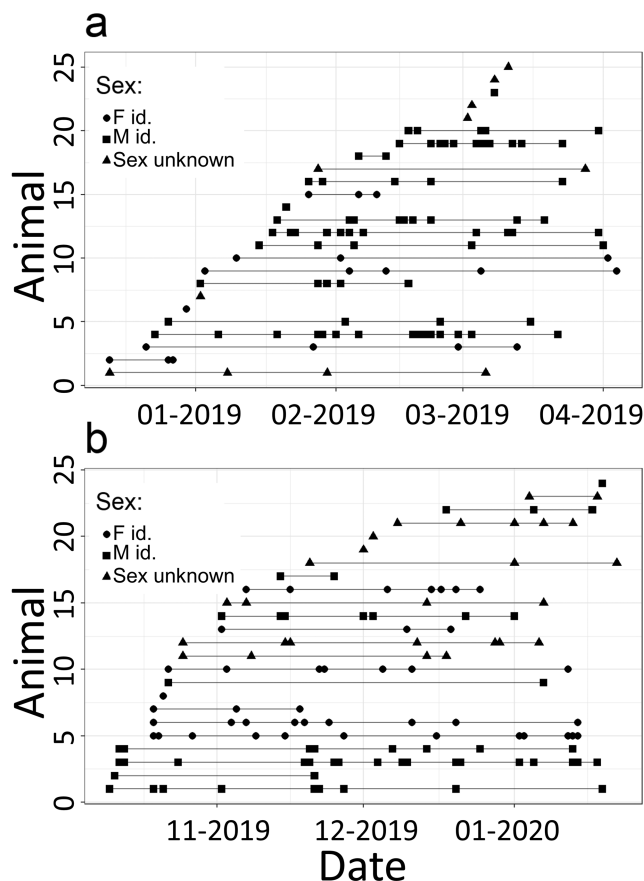
Fig. 3.—Mark recapture saturation graph with recaptures of each identified individual lynx used for spatially explicit capture recapture modeling of population parameters for the winter (panel a) and for the autumn session respectively (panel b). F and M id. stands for identified female and male individuals while Sex unknown stands for identified individuals that we were not able to determine their sex.

Table 2.—Abundance and density for Eurasian lynx in a study area in the Southern Carpathians, Romania. *N* independent is the observed number of independent lynx whose capture history we used to fit spatially explicit capture recapture models; *N* kittens is the observed number of kittens in family groups, and equated the presence of a kitten as the presence of their respective female; "Realized *N*" is the number of independent individuals within the region for the current realization of the modeling process (see Efford and Fewster 2013 for further details).

Session	*N* independent lynx	*N* kittens	Method	Regional abundance		Density (lynx/100 km²)	
				Mean ± SE	95% CI	Mean ± SE	95% CI
Winter	21	6	Realized *N*	44.12 ± 8.48	32.51 - 67.41	1.60 ± 0.39	1.00 - 2.57
Autumn	23	9	Realized *N*	48.06 ± 8.11	36.50 - 69.52	1.73 ± 0.38	1.12 - 2.66
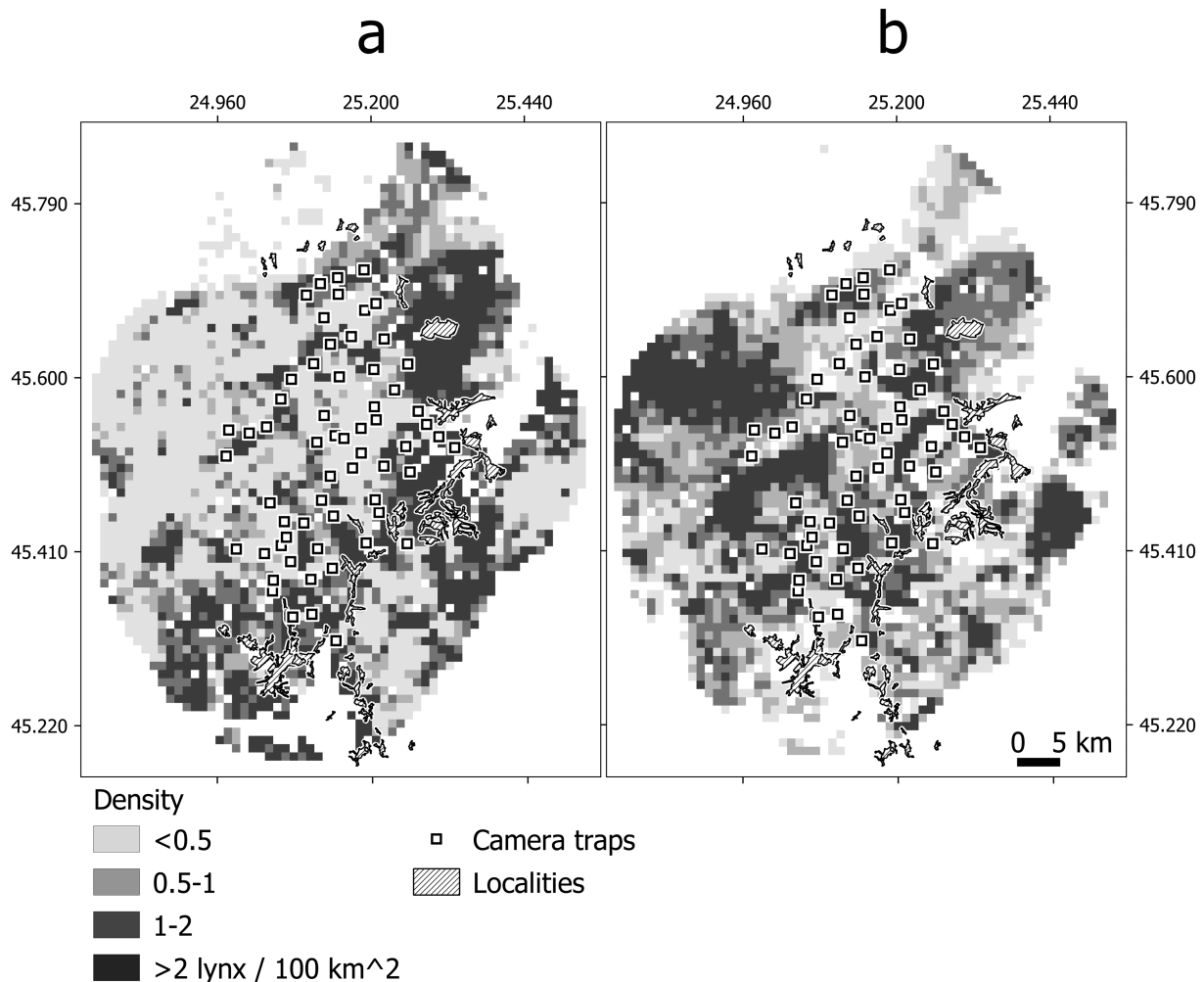
Fig. 4.—Density surface models derived through spatially explicit capture recapture for the Eurasian lynx in a study area in the Southern Carpathians, Romania. We modeled forest cover, agricultural mosaic, and terrain slope against the encounter history of 21 identified lynx during the winter, respectively, 23 during the autumn, within an effective sampling area of 2,729.5 and 2,767.4 km² for the winter (panel a) and the autumn, respectively (panel b).

in response to snow cover. High connectivity positively affected the presence of other large carnivores in the Romanian Carpathians (Roellig et al. 2014), and our results corroborate these findings. While in the Scandinavian landscape, lynx occurrence and movement was not necessarily dependent on ungulate prey movement (Walton et al. 2017), our results corroborate the finding that lynx are efficient predators and can persist in landscapes with low ungulate prey densities (Nilsen et al. 2009).

We estimated the regional abundance at 44 and 48 lynx for the winter and the autumn session, respectively. These estimates are not sex-specific, because separate predictions for males and females were limited by the difficulty in identifying the sex of all lynx at camera traps. Longer term monitoring would allow for sex identification for the majority of lynx in a studied population (Rovero and Zimmermann 2016). In addition, higher mobility of males during the reproductive season (winter) likely led to higher detection and recapture rates at cameras, for both resident and nonresident males. Lynx detected during a single

monitoring session in our encounter histories suggest that those individuals could have been nonresident animals that expanded their home range, i.e., during the breeding season. This is supported by telemetry data elsewhere in Europe, which showed that (i) males had larger territories than females (Breitenmoser-Wursten et al. 2007; Signer 2017); and (ii) there was overlap between home ranges of neighboring males: 16.2% in Jura Mountains (Breitenmoser-Wursten et al. 2007) and up to 30% in Białowieża Primeval Forest (Schmidt et al. 1997), significantly higher than the overlap between female ranges. The potential bias in recaptures of individuals that only transit the study area (nonresident) is however accounted for by including study area edge effects in the SECR models (Royle et al. 2014).

We found that lynx density varied across space and sessions in response to topography (slope), forest cover and cover of agricultural mosaic. Density hotspots shifted between the agricultural mosaic at lower altitudes correlated with less steep slopes during the winter session, and the compact forest stands at mid-altitudes with more rugged terrain during the autumn (Fig. 4). Our findings

on the shift and drivers of seasonal density patterns corroborate findings of Rozylowicz et al. (2010) and Filla et al. (2017), who investigated habitat selection based on GPS telemetry and also found a selection towards heterogeneous habitats. At lower elevations in the Romanian Carpathians, traditional low-intensity farming creates a mosaic of hayfields and orchards with significant areas of natural forest. This landscape mosaic is known to attract high densities of ungulates, such as roe deer, one of the main lynx prey species (Molinari-Jobin et al. 2007; Basille et al. 2009), as well as leporids that were found dominant in lynx diet in populations inhabiting open habitats (Mengüllüoğlu et al. 2018). In forest ecosystems similar to our study area, Herfindal et al. (2005) showed that variation in home-range size of both male and female lynx was explained by variation in roe deer density, while Schmidt et al. (1997) showed that male lynx home ranges were related to the distribution of females, whereas female home ranges were determined by availability of food resources. We did not monitor lynx in high elevation areas (above the tree line), which harbor a healthy population of another important prey species, the chamois. For this reason, the density spatial predictions might not reflect lynx space use due to chamois presence, especially during the autumn session. However, in winter, chamois also prefer lower altitudes when foraging in mid-elevation forests (Kati et al. 2020), which coincide with areas of high lynx density in our predictions (Fig. 4; Supplementary Data SD1). Moreover, the seasonal shift of lynx density toward the agricultural mosaic may be explained by a varied diet which include leporids. We found that 26% of our traps capturing lynx captured leporids too but lack of diet data for the Romanian lynx population limits inferences on leporids influence on lynx density.

Conservation and management implications.—Our results suggest that identifying individual lynx from camera trap data is feasible for the Romanian Carpathian population, and can be used as a monitoring method at broader spatial scales across Romania. Increasing detections at cameras can be achieved through pilot surveys targeted towards identifying suitable locations for lynx movement (Stewart et al. 2018). For national scale monitoring in the Romanian Carpathians, we suggest replicating the autumn monitoring scheme across several study sites representative for the entire Romanian Carpathians forest ecosystems: e.g., sites representing the compact forest landscape of the Eastern Romanian Carpathians, sites covering the rugged terrain of the Southern Carpathians, and sites located at lower altitudes in the Western Romanian Carpathians. Such surveys could be implemented at regular intervals (e.g., 5 years), and supplemented by annual reporting of track counts, a measure of relative abundance. Such a monitoring scheme will improve the national-level lynx estimates, and provide critical information on density and habitat relations for an important source lynx population for natural recolonization and reintroduction programs.

CONFLICT OF INTEREST

None declared.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Modeling workflow for lynx density and population size in a spatially explicit capture recapture framework in Southern Carpathians, Romania.

Supplementary Data SD2.—Model likelihood for different combinations of spatial detection models.

Supplementary Data SD3.—Independent lynx identified during the winter and/or during the autumn monitoring sessions, with date of first captures and category of coat pattern.

Supplementary Data SD4.—Spatial pattern of lynx recaptures at camera stations in a study area in Southern Carpathians, Romania. Note that sex is plotted in the ID of each individual where m, f, and u stand for male, female, and identified individuals but with sex unknown.

Supplementary Data SD5.—Summary of the trap revealed movement (in km) of the identified lynx males and females in Southern Carpathians, Romania. The QQ plots allow interpreting the spatial recapture patterns between sexes and seasons.

Supplementary Data SD6.—Model likelihood for different predictors we used to fit density variation in space (D surface).

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