

EURASIAN EAGLE-OWL *Bubo bubo* (Linnaeus, 1758) (AVES: STRIGIDAE) IN EASTERN SERBIA IN THE 21ST CENTURY: DISTRIBUTION, POPULATION SIZE AND DENSITY

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ABSTRACT. The Eurasian Eagle-owl represents a widely distributed but locally scarce apex predator whose biology and ecology in Serbia remain understudied. Here, we examined the spatial and altitudinal distribution, population size, and territory density of this species in Eastern Serbia. Our surveys identified 79 owl territories spread across 51 10×10 km UTM squares, resulting in a mean density of 0.5 territories/100 km². The territories were unevenly distributed, primarily concentrated in hilly terrains, river valleys and along mountain edges. The altitudinal range of identified territories spanned from 65 to 645 m, with the majority located in hilly zones below 500 m. Notably, we discovered 42 new, previously undocumented territories. Based on the collected data and habitat modelling, we estimate that the number of Eagle-owl territories in Eastern Serbia ranges from 135 to 170. Our findings contribute to a better understanding of the species' ecology and form a solid framework for future studies.

Keywords: *Bubo bubo*, conservation biology, habitat modelling, Important Bird Area, Serbia

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INTRODUCTION

Spatial distribution and population size represent the basic ecological parameters of any vertebrate species based on a fundamental quantitative unit - data on the presence (BEGON *et al.*, 1986; KÉRY and ROYLE, 2015). Understanding these parameters holds significance from both theoretical and applied approaches (NEWTON, 1979; JETZ *et al.*, 2019). From a theoretical standpoint, the distribution of a species serves as an indicator of ecological, climatic, and environmental changes across temporal and spatial scales, shedding light on both past and present ecosystem dynamics (MATVEJEV, 1950; NEWTON, 1979; HUSTON, 1994; HUNTLEY *et al.*, 2007). From a practical perspective, conservation strategies and biodiversity management highly depend on correct knowledge of species' range and population size (PUZOVIĆ, 2000; JETZ *et al.*, 2019; IUCN, 2024). Additionally, precise, georeferenced data play a critical role in identifying priority habitats, monitoring population trends, and evaluating the impacts of anthropogenic pressures on ecosystems. In the face of rapid global changes, including climate shifts and habitat loss, accurately mapping species distributions and quantifying population sizes has become increasingly critical (PERNETTA *et al.*, 1994; JETZ *et al.*, 2012). This need is particularly important for apex predators, such as owls (Strigiformes), which play crucial roles in supporting ecosystem stability and trophic dynamics (LIMA *et al.*, 2002; SERGIO *et al.*, 2008; DONÁZAR *et al.*, 2016).

Globally, owls are represented by 269 species (MELO *et al.*, 2022; MIKKOLA, 2013), of which 14 species are either regularly or occasionally recorded on the European continent (MIKKOLA, 2013). The distribution and abundance of owl species are relatively well-documented across Europe. In contrast, knowledge about these variables in Serbia and adjacent areas remains quite limited. Of the 10 owl species known to breed in Serbia, most lack detailed studies of their biology and ecology. The Eurasian Eagle-owl *Bubo bubo* (Linnaeus, 1758) emerges as one of the least studied species in the country, with virtually no dedicated research conducted to date.

The Eurasian Eagle-owl (hereinafter Eagle-owl), with a wingspan of nearly 190 cm, a body length of up to 75 cm, and a maximum body mass of 4.3 kg, is the largest owl in Serbia and one of the largest in the world (KÖNIG *et al.*, 2008; MIKKOLA, 2013). This species is distributed across the Palearctic zone, comprising 13 recognised subspecies (KÖNIG *et al.*, 2008; PENTERIANI and DELGADO, 2019). The Eagle-owl primarily inhabits sparsely populated, semi-open, mosaic landscapes with some terrain ruggedness, avoiding dense, continuous forests and large water bodies (KÖNIG *et al.*, 2008; PENTERIANI and DELGADO, 2019). It is a dietary generalist, which requires structurally complex habitats with diverse prey bases, ranging from large insects to medium-sized mammals and large birds (KÖNIG *et al.*, 2008; PENTERIANI and DELGADO, 2019; OBUCH, 2024). Globally, the Eagle-owl population is roughly estimated between 250,000 and 2,500,000 individuals (HOLT *et al.*, 2020). In Europe, the breeding population is believed to range from 19,000 to 38,000 breeding pairs, with the largest populations found in Russia, Spain, France, and Germany (BIRDLIFE INTERNATIONAL, 2017).

As mentioned earlier, specific studies on the Eagle-owl in Serbia are lacking. Only population size and trends are assessed based solely on experts' judgments. According to PUZOVIĆ *et al.*, (2015), the national population consists of approximately 380-530 breeding pairs, with 110-140 of them located in Eastern Serbia. While the species is classified globally and in Europe as *Least Concern* (BIRDLIFE INTERNATIONAL, 2017), its relatively small population size and potentially fragmented area of occupancy in Serbia, confined south of the Sava and Danube Rivers, result in its IUCN classification as *Near Threatened* on the national level (RAJKOVIĆ *et al.*, 2018).

As a top predator, the Eagle-owl has received considerable scientific attention across Europe over the past 50 years. However, notable discrepancies exist in the intensity and

abundance of regional peer-reviewed studies. For instance, this owl species has been thoroughly studied in countries such as Spain, Finland, Germany or Portugal (PENTERIANI and DELGADO, 2019). On the other hand, it remains a surprisingly understudied taxon in several countries, primarily in Eastern Europe, including Serbia. The most Serbian data regarding Eagle-owl are anecdotal, fragmented, and embedded mainly within broader faunistic inventories (e.g., RAJZER, 1904; MATVEJEV, 1938, 1950; HAM, 1980; VASIĆ and GRUBAČ, 1983; GRUBAČ *et al.*, 2013; PANTOVIĆ, 2015). Also, these studies often lack consistency in spatial coverage, temporal scope, and methodological rigour. This acute shortage of information, combined with the species' presumed rarity, ecological importance and conservation significance, justified a survey of Eagle-owl population in Eastern Serbia.

Therefore, the primary aim of this study is to provide a comprehensive assessment of the Eagle-owl population in Eastern Serbia during the 21st century by examining and analysing i) its recent and potential distribution, both spatially and altitudinally, ii) population size, and iii) territory density.

MATERIALS AND METHODS

Study area

The study was conducted in Eastern Serbia, covering a total area of 14,541 km². The Danube River flow defines the northern boundary of the study area, while the eastern boundary corresponds to the national borders with Romania and Bulgaria. To the south, the boundary was marked by a line connecting Dimitrovgrad, Babušnica, Gadžin Han, and the city of Niš. The western boundary follows the line Niš-Ražanj-Despotovac-Kostolac, marking the transition between the mountainous terrain and the plains intersected by the valleys of the Mlava, Resava, Great Morava, and South Morava Rivers. Therefore, in the broad context, the study area encompasses the Carpathian and Balkan regions of Serbia, including the Ključ and Negotin regions (RADOVANOVIĆ, 1958; DUKIĆ, 1975).

From a geological perspective, the studied region is highly diverse. It includes schists, limestones, red sandstones, river sediments, aeolian deposits, and magmatic rocks, with limestone accounting for nearly a quarter of the total area (DUKIĆ, 1975). The terrain is predominantly hilly and mountainous, characterized by folded mountain ranges interspersed with numerous river valleys and small to medium-sized basins (RADOVANOVIĆ, 1958; KNEŽEVIĆ, 2013). The lowest point of the study area is at just 28 m above sea level near the confluence of the Timok and Danube Rivers, while the highest point is Midžor (2,169 m) on Stara Planina Mt.

The hydrographic network, a vital component of the biogeographical environment, is relatively well-developed, featuring numerous creeks and rivers that predominantly follow a pluvial-nival flow regime (RADOVANOVIĆ, 1958; KNEŽEVIĆ, 2013). Major river basins include the Danube, Timok, Mlava, Resava, Nišava, and Pek. Due to the region's landscape heterogeneity, the climate of Eastern Serbia is relatively complex, with a mix of temperate, steppe, and continental conditions as well as a mountainous climate above 1,000 m. Summers are moderately warm, while winters are cold and windy. The prevailing winds blow from the northwest, often "channelled" by the mountain massifs and terrain configuration (DUKIĆ, 1975; DUCIĆ and RADOVANOVIĆ, 2005). In the Negotin area and along the Danube, the "košava" is the most common wind. Annual precipitation varies between 500 and 700 mm in lower altitudes, reaching over 1,000 mm in mountainous areas (DUKIĆ, 1975). Snow cover exceeding 1 cm lasts 20-40 days in lowlands and increases linearly with elevation, persisting up to 180 days on the highest peaks of Stara Planina Mt (DUKIĆ, 1975; DUCIĆ and RADOVANOVIĆ, 2005).

Settlements in the study area are primarily found in basins and river valleys, with few situated on mountain slopes. Eastern Serbia is the least populated region in the country, home to less than 20% of Serbia's total population. Currently, the population density is approximately 70 inhabitants per km² (KNEŽEVIĆ, 2013).

Data collection

The data on the presence of the Eagle-owl were collected over nearly a quarter-century, from January 1, 2002, to June 15, 2024. However, most of the data (83%) were collected after 2013, when research on this species became more standardised and systematic, while field surveys were substantially intensified. This extensive fieldwork primarily focused on the municipalities of Veliko Gradište, Golubac, Knjaževac, Zaječar, Sokobanja, Svrljig, Pirot, and parts of Negotin. At the same time, the rest of the study area was partly and unevenly covered.

The presence of territories occupied by an individual or pair of Eagle-owl was determined using one or a combination of several standard methods (MYSTERUD and DUNKER, 1982; PENTERIANI *et al.*, 2004; DELGADO and PENTERIANI, 2006; PÉREZ-GARCÍA *et al.*, 2012). These methods included (i) habitat surveys to identify suitable territorial grounds, (ii) passive auditory monitoring of adult territorial birds, and (iii) vocalisation surveys to detect fledglings. The first method focused on surveying habitats such as rocky outcrops, cliffs, scree slopes, and sparsely vegetated steep terrains, aiming to detect individuals, nest scrapes, pellets, or plucking/feeding micro-sites (Figure 1). These surveys were conducted year-round. However, particular focus was placed on the period from February to September, as it corresponds to the nesting season when owl individuals are more closely associated with core area boundaries (i.e. close to the nesting scrape). In addition to natural sites, artificial structures such as quarries and borrow pits were also inspected, as they are recognised as breeding sites in neighbouring countries (PROMMER *et al.*, 2018; GOLNAR, 2019; MILCHEV *et al.*, 2019; JEČMENICA *et al.*, 2022) and elsewhere in Europe (MARCHESI *et al.*, 2002; PENTERIANI and DELGADO, 2019; LAPSHIN *et al.*, 2022). ii) Passive acoustic surveys, focusing on the vocalisations of males or pairs during evening and nighttime hours. This method was utilised during the pre-breeding period, from late November until the end of March, when Eagle-owls are most vocal in the central Balkans. iii) Passive auditory surveys for fledgling vocalisations were conducted from late May to mid-August during evening hours. Positive detection by at least one of these three methods was considered valid, and the surveyed site was classified as an Eagle-owl territory.

To refine the dataset and address spatial gaps, we employed a citizen science approach, contacting ornithologists via email and social media. Their contributions, though scarce, provided valuable observations and records, expanding our dataset with supplementary inputs. Additionally, literature reviews on the species' presence, including books, scientific articles, and technical reports (e.g., GRUBAČ *et al.*, 2013; PANTOVIĆ, 2015), were also conducted.

We gathered minimal set of geographical and ecological attributes for all collated data, including toponym name, latitude and longitude, elevation (altitude), and municipality. Elevation of each territory was rounded to the nearest 5 meters, and sites were classified as lowland (<200 m), hilly (200-500 m), or mountainous (>500 m). These attributes were organised into MS Excel spreadsheets for further processing and visualisation.

Georeferenced data and associated information have been excluded from this article to address conservation concerns. Instead, they have been stored in the National Biodiversity Database managed by the Institute for Nature Conservation of Serbia (Belgrade) for further maintenance.

Data processing and statistical analysis

After collating the data into tables, further processing and statistical analysis were conducted. Indicators of ecological density and spatial distribution of Eagle-owl territories were included the Nearest Neighbour Index (R) (CLARK and EVANS, 1954), the G-test (BROWN and ROTHERY, 1978), and the Isolation Index (Si) (CARRETE *et al.*, 2006). The Nearest Neighbour Index (R) characterises spatial distribution patterns as uniform ($R > 1$), random ($R = 1$), or clustered ($R < 1$) (CLARK and EVANS, 1954). The Isolation Index (Si) ranges from 0 to 1, representing more isolated and more connected territories, respectively (CARRETE *et al.*, 2006). The G-test measures spatial regularity, with values ranging from 0 to 1, where values greater than 0.65 indicate a regular distribution (BROWN and ROTHERY, 1978). All three metrics were calculated as Euclidean distance, rounded to the nearest 5 meters using QGIS version 2.18. The centre of each territory was defined primarily by a plucking site or nesting scrape. However, in cases of large gorges with multiple nest micro-locations, the barycentre was used. The absolute density of the Eagle-owl subpopulation in Eastern Serbia was calculated as the number of territories per 100 km². To estimate the population size, we used the predicted favourable habitat by MaxEnt (see below) in combination with the known home range size of a single territory. Preliminary research conducted in the Sokobanja basin in Eastern Serbia, based on satellite telemetry of five tagged Eagle-owl males, indicates that the home range of a single territory varies between 12 and 15 km².



Figure 1. Traces indicating the presence/occupancy of a site by the Eurasian Eagle-owl *Bubo bubo* in Eastern Serbia: 1) typical, loosely compacted pellets, composed of hedgehog hair and spines, deposited on favourite perch, 2) a plucking site on the cliff edge, 3) food remains (bones and fur) at the nesting micro-location after a nesting period, and 4) a nest with a single 32-day-old chick (photo by Draženko Z. Rajković, 2023 and 2024).

To model the potential distribution of the Eagle-owl in Eastern Serbia, a dataset of 79 precise georeferenced presence records (latitude and longitude) was used, in combination with a comprehensive set of widely applied climatic, habitat, and topographic variables (Table 1). The number of georeferenced records was adequate and exceeded the threshold for reliability (HERNANDEZ *et al.*, 2006; PAPEŞ and GAUBERT, 2007). All raster data for the environmental variables were reprojected into the WGS 84 coordinate system (UTM Zone 34N) during preprocessing, with a resolution of 100×100 m.

Table 1. Bioclimatic and other environmental variables were used to model the potential distribution of the Eurasian Eagle-owl *Bubo bubo* in Eastern Serbia.
Variable sources: (JARVIS *et al.*, 2008; EEA, 2012; FICK and HIJMAN, 2017)

Variable code	Variable explanation
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (×100)
BIO4	Temperature Seasonality (Standard Deviation ×100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter
CLC	Land classes according to the CORINE classification
ELE	Mean elevation of the grid cell
SLP	Mean slope of the grid cell

The distribution modelling was performed using MaxEnt version 3.4.3 (PHILLIPS, 2017), a machine-learning software designed to generate presence-only distribution models (PHILLIPS *et al.*, 2006; PHILLIPS and DUDIK, 2008). MaxEnt strives to identify the distribution model with maximum entropy using a wide range of statistical tuning options. As the primary goal of this study was to estimate the approximate area of potential distribution without delving into detailed analyses, most MaxEnt settings were left at their default values. We used a linear feature transformation, with the number of iterations set to 1,000 and the number of random background locations set to default. The model was cross-validated with 10 replicates. Training data included 75% of the presence locations, while the remaining 25% were used for model validation. The logistic output was selected, providing the probability of Eagle-owl presence for each 100×100 m grid cell on a scale from 0 to 1. The predictive reliability of the distribution model was assessed using the Area Under the Curve (AUC) and True Skill Statistic (TSS) metrics. Predictive accuracy was considered acceptable when AUC > 0.7 and TSS > 0.4 (SWETS, 1988; HODD *et al.*, 2014).

Due to the pronounced skewness and to minimise the influence of extreme values, all continuous variables were log-transformed (*log10*). Descriptive statistics like dispersion and central tendency measures were presented as mean, standard deviation, range, and median. The significance threshold for statistical tests was set at $p \leq 0.05$. Data analysis and result visualisation were performed using RStudio (RSTUDIO TEAM, 2022). Figure processing was conducted using the vector graphics software Inkscape version 1.4. The normality of the distribution decides the choice between parametric and non-parametric statistical tests, assessed through Levene's homogeneity of variance test (LEVENE, 1960).

RESULTS AND DISCUSSION

Spatial and altitudinal distribution

As shown in Figure 2, the territories of the Eagle-owl are distributed across most parts of Eastern Serbia. However, their distribution was notably irregular. The Eagle-owl appears to be entirely or largely absent from high mountain ranges and extensive, dense forest complexes, such as Homolje, Kučaj-Beljanica, Deli Jovan, Rtanj, Bukovik, Suva, and Stara Mt. Instead, our findings show that Eagle-owl territories are primarily found in river valleys, basins, foothills, and along mountain edges. This distribution pattern is likely driven by the availability of open and semi-open areas essential for hunting, nesting micro-locations and climatic conditions that become increasingly scarce and unfavourable at higher altitudes. These findings are consistent with known ecological preferences from other European studies (KÖNIG *et al.*, 2008; PENTERIANI and DELGADO, 2019).

Overall, discovered territories within 51 distinct UTM squares (10×10 km) cover 27.4% of the 186 squares in the study area. The number of territories per occupied square ranged from one to four (Figure 2). According to data from the Red Book of Fauna-Birds (RAJKOVIĆ *et al.*, 2018), we recorded at least 42 new territories in 29 previously undocumented UTM squares. These results underline a significant increase in research intensity focused on the Eagle-owl population in Eastern Serbia. They also highlight the importance of employing appropriate methodologies in studying elusive, nocturnal and rare species, such as the Eagle-owl in order to understand better and determine their spatial distribution.

Historically, specific breeding sites along the Kravljanska River and Vratna gorge have likely been occupied for the past 45-50 years (HAM, 1980; VASIĆ and GRUBAČ, 1983). In some locations, like the vicinity of Boljetin, Majdanpek (DOMBROWSKI, 1891), and Niš (RAJZER, 1904), territories have persisted for over 120 years. These longstanding occupied territories may be described as "prime breeding grounds", which underlines the significance of continuous monitoring and conservation efforts to ensure the long-term protection of the mentioned locations. The core Eagle-owl territories were situated along valleys and basins of major rivers, including the Danube, Pek, Timok, Sokobanjska Moravica, Nišava and adjacent hilly slopes. The map (Figure 4) suggests additional areas recognised as potentially suitable habitats but without recorded territories. This discrepancy likely arises from insufficient survey efforts rather than the species' true absence. Inadequately assessed or sparsely surveyed regions include localities within the municipalities of Bor, Kladovo, Despotovac, Boljevac, and Kučevo. Addressing these spatial gaps through more comprehensive surveys in future studies is essential for an improved understanding of the species distribution.

Regarding vertical distribution, the average altitude of the territories was 338 ± 159 m (med=350 m, range: 65-645 m). These results are pretty consistent with studies from neighbouring nearby countries, such as Slovenia (TOME, 1996; GOLNAR, 2019), Austria (GRÜLL *et al.*, 2010) and Bulgaria (HRISTOV *et al.*, 2007). In Slovenia, Eagle-owl territories

are typically found at elevations between 300 and 600 m, while in Bulgaria, they range from 100 to 400 m. Similarly, Eagle-owl occupies altitudes between 256 and 505 m in Austria, further confirming its strong affinity for mid-elevation zones. There was no significant difference in altitude between territories located inside and outside of Important Bird Areas (IBAs) (Welch t-test: $t=0.58$, $p=0.56$). From a conservation planning perspective, this result indicates that management strategies or habitat interventions for Eagle-owl, within and outside of IBAs, may not need to account for elevation differences but should instead focus on other ecological factors more relevant to the species' ecological needs. Overall, 24% of territories were located in lowlands, 57% in hilly regions, and only 19% in mountainous areas (Figure 3). These differences in altitudinal distribution between relief zones were statistically significant (Kruskal-Wallis test: $\chi^2=61.99$, $p<0.001$).

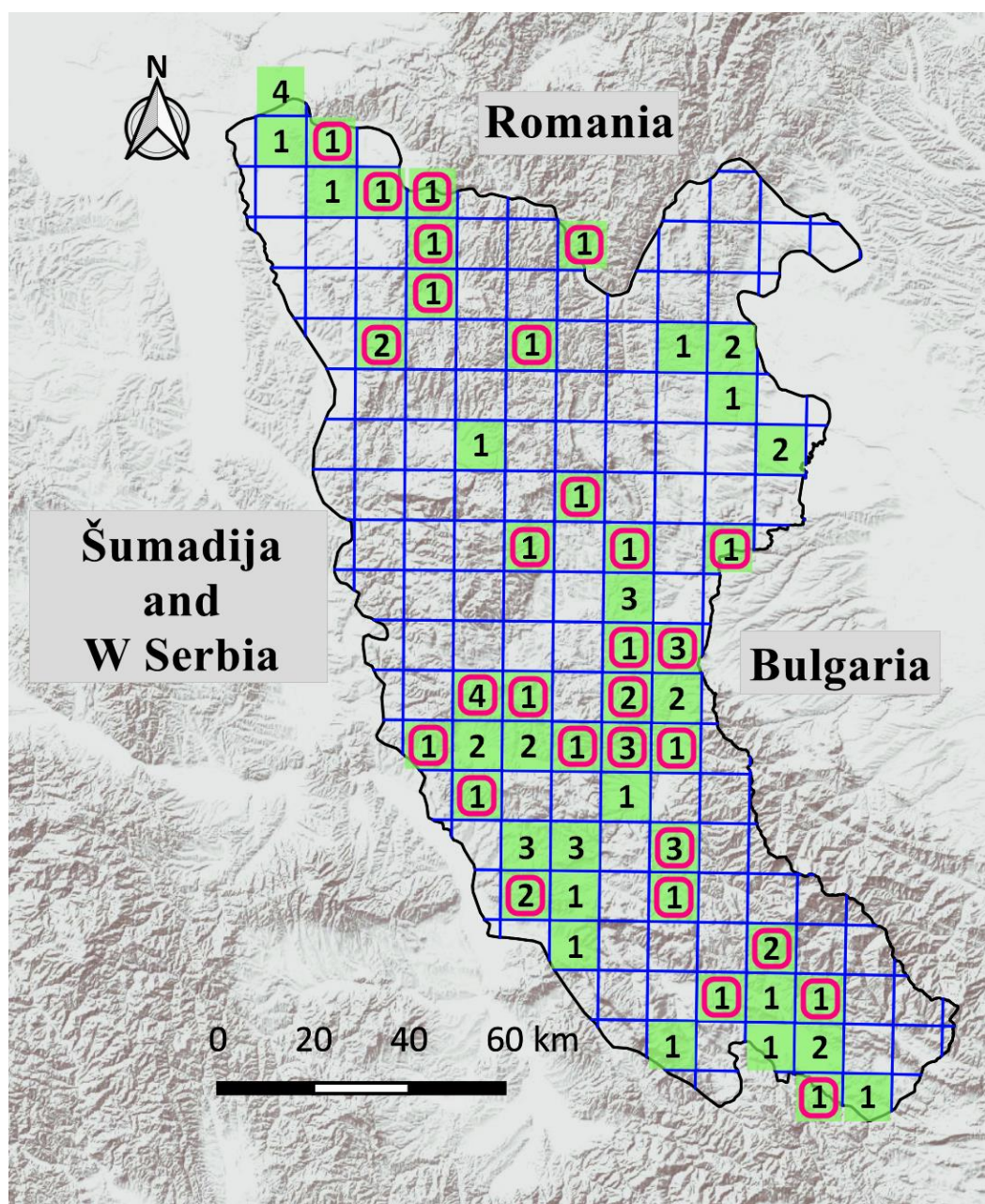


Figure 2. Numbers of the Eurasian Eagle-owl *Bubo bubo* territories concerning the UTM grid 10×10 km in Eastern Serbia (N=79). The numbers outlined in red represent new, previously unrecorded territories, using the species chapter in the Red Book of Fauna of Serbia III – Birds (RAJKOVIĆ *et al.*, 2018)

Altogether, the obtained findings show that the Eagle-owl occupies a relatively wide range of altitudes. However, the hilly areas contain the majority of territories. These findings align with the species' known ecological requirements, favouring moderately undulating landscapes likely due to the favourable combination of suitable nesting sites and semi-open areas for hunting (MIKKOLA, 2013; PENTERIANI and DELGADO, 2019). The lowest recorded territory was 65 m above sea level near Negotin, while the highest was at approximately 645 m on the slopes of Ozren Mt. Therefore, we can assume that the current maximum altitude in Eastern Serbia is approximately 700 m, with territories at higher elevations being exceptions rather than the norm. Although no significant difference in elevation was found between territories inside and outside IBAs, the vertical distribution among lowland, hilly, and mountainous landscapes was statistically significant. These findings highlight the importance of the hilly zone as a key habitat for population conservation. The fewer territories in lowland and mountainous areas likely result from denser, less favourable habitats, relatively high anthropogenic pressure, and low prey abundance and availability.

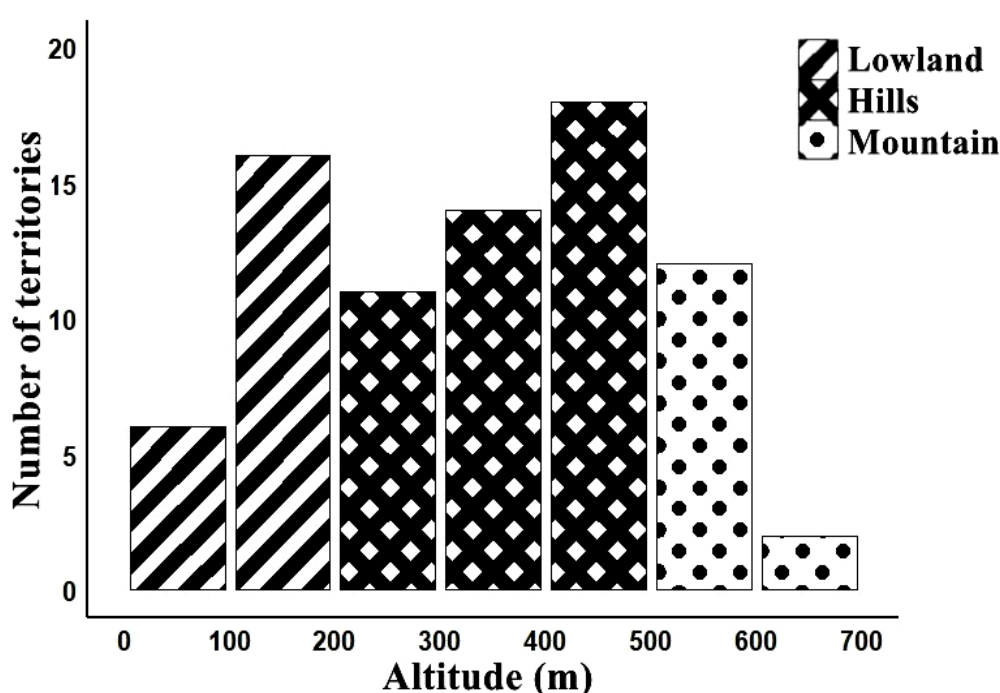


Figure 3. Altitudinal (vertical) distribution of Eurasian Eagle-owl *Bubo bubo* territories in Eastern Serbia (N=79)

The mean distance between centroids of neighbouring territories was $5,567 \pm 4,137$ m (med=4,120 m, range: 1,070-20,670 m), which aligns with findings from other European regions with low and moderate Eagle-owl densities (PENTERIANI and DELGADO, 2019). For example, in some parts of Switzerland (ARLETTAZ, 1988), France (CUGNASSE, 1983) and Sweden (OLSSON, 1997), where territory densities are low, the mean distance between neighbouring territories exceeds 8 km, while in high-density areas of Spain, distance can decrease to as 1 km or even less (PÉREZ-GARCÍA *et al.*, 2012; PENTERIANI and DELGADO, 2019). The clustering of territories in our study suggests a sufficiently optimal balance between resource availability and the need to minimize territorial conflicts. Interestingly, the majority of territories (63.3%) were located closer than the mean distance, indicating a skewed distribution with a significant proportion of territories clustered at smaller distances.

Within IBAs, the average distance between territories was $5,441 \pm 4,365$ m (med=4,040 m, range: 1,070-21,740 m). Statistical analysis indicated no significant distance difference

between neighbouring territories inside and outside IBAs (Welch t-test: $t=0.78$, $p=0.44$). This finding suggests that IBAs, while designed to protect critical habitats and species, may not necessarily alter the spatial arrangement of Eagle-owl territories. Instead, the factors driving territory spacing appear consistent across different landscape protections, likely driven by intrinsic ecological requirements rather than conservation area designations. The relationship between altitude and nearest neighbour distance was assessed using linear regression. The model revealed a weak but statistically significant negative relationship ($\beta=-6.81$, $p=0.02$), with $R^2=0.07$. These findings indicate that altitude changes can explain 7% of the variance in nearest neighbour distance. Therefore, the nearest neighbour distance decreased by 7 m for every meter increase in altitude. Although the model was significant ($F=5.64$, $p=0.02$), the low R^2 suggests that other factors may contribute to the variation in nearest neighbour distance. Further investigation incorporating additional predictor variables may improve the explanatory power of the model in order to better understand the relationship between spatial distribution and altitude. Hence, observed distribution patterns of Eagle-owl territories suggest that other environmental factors, such as prey density, habitat structure, and human disturbance, may be more important in determining territory disposition and spacing.

The implications of these findings are twofold. First, the absence of significant spatial differences between IBAs and non-IBAs highlights the importance of broad-scale habitat conservation that transcends designated protected areas. Second, the lack of altitude-driven spatial patterns shows that Eagle-owls exhibit ecological flexibility in territorial establishment, allowing them to adapt to various topographical conditions, provided other habitat requirements are met.

Numbers, density and population size

Altogether, we conducted a detailed inspection of 128 randomly selected sites distributed across Eastern Serbia. We identified Eagle-owl territories at 61.7% ($N=79$) of these locations. The nearest-neighbour index showed a clustered distribution pattern ($R=0.13$), and this deviation from randomness was confirmed statistically ($z=-2.28$, $p<0.001$). However, no significant spatial isolation of pairs was detected ($S_i=0.79$). The G-test value of 0.39 indicates that distribution is closer to clustering or randomness than uniformity. This result likely reflects specific habitat preferences and ecological factors, such as habitat openness and terrain ruggedness, which influence territory establishment.

The overall density of Eagle-owl territories was 0.5 per 100 km², varying across different parts of the study area. This density estimation can be considered conservative because the entire study area was not surveyed equally, and additional territories are undoubtedly present. However, even with the inclusion of newly discovered territories in the future, the density is unlikely to significantly exceed one territory per 100 km². Locally, the highest densities, exceeding three territories per 100 km², were recorded in the Sokobanja and Zaječar basins, pointing out the importance of these areas as important habitats for the species. Still, presented densities are noticeably lower than in most European studies. The density of Eagle-owl territories in Eastern Serbia is low compared to the rest of Europe, where the mean density is 5.5 ± 8.2 per 100 km² (PENTERIANI and DELGADO, 2019). However, European studies showed highly substantial variation (range: 0.01–40, med=2). For example, densities often exceed 10–20 pairs/100 km² in the Mediterranean region (e.g., PÉREZ-GARCÍA *et al.*, 2012; BARIŠIĆ *et al.*, 2016) while in most parts of central, eastern and northern Europe (see PENTERIANI and DELGADO, 2019) is relatively close or similar to our study. On the local level, the higher densities observed in the Sokobanja and Zaječar basins indicate the presence of (sub)optimal habitats with abundant prey and suitable nesting sites. This finding highlights the critical role of prey availability and landscape heterogeneity in shaping the Eagle-owl population, providing a viable explanation for its distribution and density patterns. Similar

justification has been noticed in Spain, where European rabbit *Oryctolagus cuniculus* abundance has been a regulating factor for Eagle-owl populations (FERNANDEZ-DE-SIMON *et al.*, 2014).

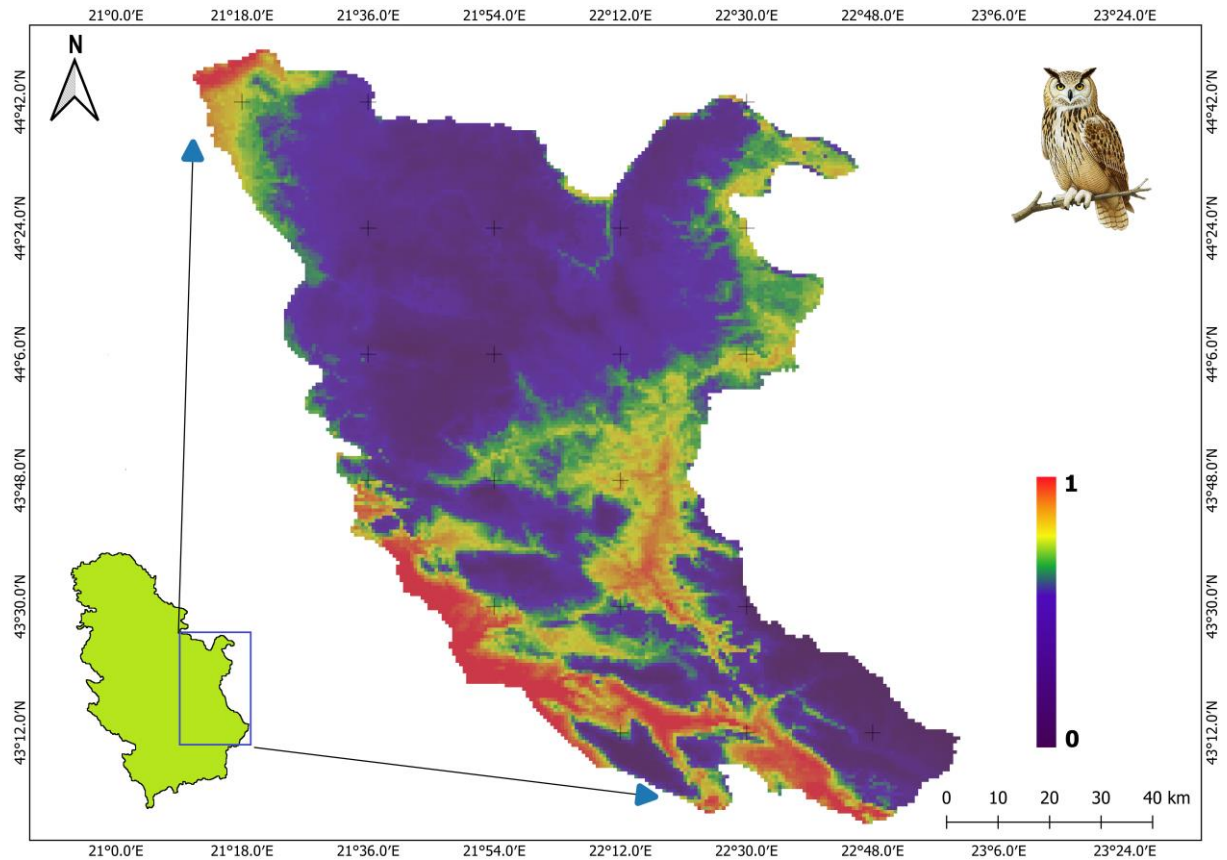


Figure 4. Map of suitable grid cells for the Eurasian Eagle-owl *Bubo bubo* predicted by MaxEnt modelling. Values approaching one (red colour) indicate the highest probability of territory presence

Within 13 Important Bird Areas (IBAs) situated partially or entirely in the study area, 61 territories (77.2%) were recorded. The territories were denser in the IBA than the overall study area (Welch t-test: $t=2.29$, $p=0.04$), averaging 1.6 territories per 100 km² (med=0.8; range: 0.2-6.2). Only 14% (N=11) of the total discovered territories are located within the borders of nationally protected areas. Three territories are situated within the boundaries of "Đerdap National Park" and "Stara Planina Nature Park", while an additional five areas each contain one territory. The findings further confirm the uneven spatial distribution of Eagle-owl territories, as highlighted in the previous section of the article. Furthermore, the obtained results have significant implications for conservation planning. While IBAs are crucial for supporting high-quality habitats, the data underscore the need for landscape-scale conservation strategies that address habitat quality both within and outside IBAs. Additionally, the clustered distribution of the Eagle-owl population in Eastern Serbia suggests that conservation efforts should prioritize key areas with high habitat suitability and connectivity to support territory establishment and reduce potential risks of population fragmentation.

Our MaxEnt distribution model showed acceptable discriminatory power (AUC=0.72, TSS=0.48). The likelihood of Eagle-owl presence decreased with increases in forest cover, annual precipitation, and elevation, and it increased with annual mean temperature and terrain steepness. Highly suitable habitats for Eagle-owl cover approximately 2,265 km², suggesting a potential for 151-189 territories under ideal conditions. However, taking into account the

clustered distribution and the fact that possibly about 10% of territories remain unoccupied annually (VUČANOVIĆ, 2022), we estimated the number of occasionally or constantly occupied territories to be around 135-170. The most suitable areas and patches for Eagle-owl in Eastern Serbia are concentrated along river valleys and lowland and basin edges in the central, southern, southwestern, and northwestern regions of the study area (Figure 4).

Although our study does not investigate the population size across the whole of Serbia, it provides a solid base for future research, additional assessments and corrections at the national level. The previous estimation made by PUZOVIĆ *et al.*, (2015), which suggested there are 110-140 Eagle-owl breeding pairs in Eastern Serbia, aligns closely with our findings. However, at the national level, the estimate of 380-530 breeding pairs appears to be an overestimation compared to the data presented here, especially considering that Eastern Serbia serves as the species' stronghold. For example, Western and Southwestern Serbia, assumed to host around 40% of the national population (PUZOVIĆ *et al.*, 2015), lack substantial evidence to support such claims (e.g., JANKOVIĆ *et al.*, 2013/2014; PANTOVIĆ, 2015; RUDIĆ *et al.*, 2016). Moreover, higher precipitation and the colder climate in Western Serbia are less suitable for Eagle-owls, which, according to our model, prefer drier, warmer landscapes on lower altitudes. The scarcity of records from Western Serbia, combined with a thorough census in the eastern part of the country, suggests that the national population is likely significantly lower than previously estimated. Given these findings and doubts, it is essential to reassess the population estimate to ensure accurate conservation planning and management.

CONCLUSIONS

This study provides the first comprehensive data and analysis of the spatial and altitudinal distribution, population size and density of the Eagle-owl in Serbia. Its spatial distribution shows a clustered pattern and predominantly occupies river valleys, foothills, and basin edges, avoiding high mountain ranges and dense forests. The findings emphasize the importance of open and semi-open habitats for Eagle-owl, aligning with ecological requirements observed in other European studies. Altitudinal distribution analysis confirms Eagle-owls' adaptability across a wide range of elevations, with most territories concentrated in hilly areas. With 79 identified territories, including 42 newly recorded, the estimated density remains low, significantly below the European average. However, local variations suggest that certain areas serve as strongholds for the species on the regional level. The MaxEnt model highlights suitable habitats covering approximately 2,265 km², with a potential for 135–170 occupied territories. This study also underscores the conservation significance of IBAs, which host 77.2% of the recorded territories. However, effective conservation strategies must be established and strengthened within IBAs, where protection measures and management actions are currently lacking and beyond their boundaries, to maintain habitat connectivity and mitigate fragmentation risks. Moreover, the clustered distribution of territories and the variability in density across different regions reflect the critical influence of prey abundance, habitat structure, and human disturbance on territory establishment. Future research should focus on under-surveyed regions and habitat preference and quality assessments to refine conservation priorities and ensure the long-term viability of the Eagle-owl population.

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