

Research article

Beyond bats: hidden mammalian biodiversity in Bulgarian caves

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Abstract: Caves in Bulgaria have been studied primarily for their bat fauna, and the occurrence of other mammals in subterranean environments has remained largely unsynthesised. Here we compile and analyse records of non-volant mammals obtained during cave surveys and bat-monitoring activities conducted between 1993 and 2026. The dataset comprises 214 records of 14 taxa from 29 caves, based on direct observations, pitfall trapping, camera trapping, tracks and scats. Most records originate from the entrance and twilight zones, whereas deeper cave sectors were only rarely used. The assemblage is dominated by facultative cave visitors: two species *Glis glis* (Linnaeus, 1766) and *Martes foina* (Erxleben, 1777), both of which were classified as common, while most taxa were rare or accidental. Visiting caves for shelters and roosting by *Rupicapra rupicapra balcanica* (Bolkay, 1925) is a rarely documented phenomenon. Data from camera traps in a small cave in the Rhodope Mountains indicate that different chamois individuals frequently visit underground cavities, using them as shelter and resting sites. Pitfall data indicate strong seasonality in small-mammal detections, with captures concentrated in the warmer months and very limited winter representation, whereas winter surveys more frequently revealed the presence of medium and large mammals. Several records, including direct observations and feeding evidence, indicate opportunistic predation on bats by carnivores. These results show that the contemporary diversity of non-chiropteran mammals using Bulgarian caves has been underestimated. The concentration of records in ecotonal cave zones indicates consistent spatial overlap with bat roosts, highlighting the need to consider the broader mammalian assemblage in cave conservation and assessments of zoonotic risk in subterranean ecosystems.

Keywords: cave ecology, carnivores, non-volant mammals, shrews, recent fauna, rodents, subterranean habitats

Introduction

Caves are widely recognised as key habitats for bats, providing essential conditions for roosting, hibernation, breeding, and seasonal movements (Kunz, 1982). In contrast, the use of subterranean environments by non-volant mammals has received far less attention, despite increasing evidence that a wide range of terrestrial species regularly exploit caves on a temporary or seasonal basis (Roper, 2010; Culver & Pipan, 2019; Vernes & Davos, 2022; Deleva et al., 2023). Forming a distinctive ecotone between epigeal and hypogeal environments, caves are characterised by a relatively stable thermal regime, high humidity, and protection from climatic extremes, creating favourable microclimatic conditions that can be exploited for resting, denning, overwintering, and occasional foraging (Prous et al., 2004; Moseley, 2009). Numerous studies have shown that small mammals and carnivores occur most frequently in entrance and twilight zones, where surface and subterranean environments overlap (Romero, 2009; Prous et al., 2015; Marchewka & Postawa, 2023). In such settings, some species may also prey opportunistically on bats at roosts or during emergence (Twente, 1955; Labadie et al., 2025; Rauch et al., 2025). Fossil data further demonstrate that the association between terrestrial mammals and caves dates back at least to the Pleistocene, indicating that the ecological use of subterranean shelters by non-flying mammals is both widespread and long-standing (Beron, 2006; Dudin et al., 2011; Churcher, 2020; Boev et al., 2024). Nevertheless, the functional importance of caves for these taxa remains insufficiently understood.

Across south-eastern Europe, biospeleological research has traditionally focused almost exclusively on Chiroptera. As a result, even basic information on the diversity and occurrence of other mammals in caves is fragmented. Bulgaria exemplifies this imbalance. To date, 26 species of cave-dwelling bats have been reported from the country (Beron, 2015), reflecting decades of targeted research and monitoring. By comparison, published data on other mammals using caves are sparse and largely incidental. Available records indicate the presence of only a limited number of non-chiropteran species. Among Carnivora, the wildcat *Felis silvestris* (Schreber, 1777) has been reported from Suhi Pech Cave. The red fox *Vulpes vulpes* (Linnaeus, 1758) has been documented from a small cave near Beledie Han and from Starshelitsa Cave (Gueorguiev & Bekchiev, 2009), with addi-

tional evidence from Spropadnaloto Cave based on scats (Beron, 2015). The Eurasian badger *Meles meles* (Linnaeus, 1758) has been observed deep within Futyovskata Cave, approximately 500 m from the entrance (Beron, 2015). Rodents are similarly poorly represented in the literature, with the edible dormouse *Glis glis* (Linnaeus, 1766) reported from Malkata Yama Cave and the wood mouse *Apodemus sylvaticus* (Linnaeus, 1758) from Razhishka Cave and Golyamata Vrazha Dupka. These isolated observations clearly indicate that caves in Bulgaria are utilised by a broader spectrum of mammals than is commonly recognised, yet their overall diversity and ecological roles remain inadequately characterised.

Importantly, much of the currently available information derives indirectly from long-term monitoring programmes focused on caves of national and international importance for bat conservation. During these surveys, non-chiropteran mammals have often been recorded opportunistically, particularly in winter, when bats are in torpor, and caves may represent predictable and energetically favourable environments for other mammals, including potential predators. Although individually scattered, these records collectively form a substantial body of evidence that has not previously been synthesised. The present study seeks to address this gap by compiling and critically analysing available records of non-volant mammals from Bulgarian caves. By providing the first integrated overview of their diversity, spatial distribution, and patterns of cave use, the study aims to draw attention to the broader mammalian component of subterranean ecosystems in Bulgaria and to underline its potential relevance for bat conservation and cave ecosystem functioning.

Material and methods

Study scope and field methods

Records of non-volant mammals from Bulgarian caves were compiled for the period 1993–2026. In total, 29 caves distributed across the country were included in the analysis. The dataset integrates both systematic sampling and opportunistic observations accumulated during speleological and faunistic surveys. Since no unified methodology for recording mammal presence in caves was applied during the entire study period, the collected data originate from different sources and sur-

vey approaches, and partly reflect incidental findings accumulated over time. Mammal presence within caves was recorded during separate studies conducted during the aforementioned period: (i) direct visual observations during cave visits, (ii) identification of tracks and other field signs, (iii) small mammal bycatch in invertebrate-targeted pitfall trapping, primarily in entrance zones and accessible passages (2022), (iv) camera trapping at selected sites (2022–2025), and (v) identification of scats and other remains (2021–2026). Therefore, the dataset should be interpreted primarily as records of mammal occurrences rather than standardised estimates of individual abundance, except for the incidental pitfall-trap bycatch, where individual specimens were recorded.

Pitfall traps (originally intended for invertebrate sampling) were deployed year-round in three large caves supporting substantial bat colonies – Devetashkata Cave (N 43.2, E 24.8), Parnitsite (N43.2, E 24.4) and Orlova Chuka (N 43.5, E 25.9). In each cave, two transects of five pitfall traps were installed (ten traps per cave). Traps within each transect were spaced at 5 m intervals. The first transect was positioned near the cave entrance but within the dark zone, while the second transect was placed in the main gallery in proximity to the bat colony. In Devetashkata Cave, both transects were located close to the bat colonies, with the second transect additionally situated near the cave river within the main gallery. In Parnitsite Cave, both transects were positioned near the cave river. Small mammals were recorded only as incidental bycatch in these invertebrate-targeted traps, and no species of conservation concern were involved. The specimens were subsequently integrated into the scientific collections of the National Museum of Natural History, Sofia (NMNHS-BAS).

Two camera traps were deployed in caves. The first cave is located in a predominantly coniferous forest near Gyuvren Village (N41.6, E24.4). It has a wide entrance (~3 m high, 5 m wide) and a depth of approximately 14 m. A single camera trap was mounted on a vertical wall 2 m from the entrance and oriented towards it. The camera operated from September 2022 until November 2022. The second cave is situated on a ridge in predominantly beech-dominated broadleaf forest in the Central Balkan Range (N42.7, E25.1). It is a through-cave with two narrow entrances on opposite sides of the ridge, approximately 27 m apart. The interior forms a passage high enough for a person to walk upright. Two camera traps were

installed near the midpoint of the cave, each facing one of the entrances, and operated almost continuously from 28 September 2023 to May 2025.

Data treatment and analysis

The curated analytical dataset is available as [Supplementary material 01](#) . Each independent observation event was treated as a single record. Standard faunistic practices typically relied on the total number of independent observations to determine range. However, in our case, since continuous monitoring (e.g., with camera traps) exponentially increases the number of records compared to discrete bycatch sampling (e.g., pitfall traps), using raw observation counts biases dominance metrics toward heavily monitored sites. Consequently, we assessed the faunal structure primarily using naïve occupancy (Soto-Werschitz et al., 2023), in our case, different cave sites where a given species was found for 29 sites surveyed. Excluding direct observations, our sampling methods (pitfalls, camera traps, tracks and scats) were concentrated at 9 of the 29 sites, resulting in an observed sample coverage of 31%. Considering this, the estimated sample coverage was established at 26–38% (Brose et al., 2003). The species richness of the cave was defined as the number of different mammal taxa recorded at that site. Based on site occurrence, species were classified into modified frequency categories: widespread (occurrence in ≥ 11 sites (more than 38%), common (occurrence in 7–11 sites), rare (occurrence in 4–6 sites), and occasional (occurrence in < 3). Each species record was treated as a single occurrence, except for pitfall trap data, where individual counts were used because specimens could be reliably distinguished.

Temporal patterns were evaluated using annual totals of records. Seasonal analyses were based exclusively on observations for which the season could be determined. Records were assigned to four seasons (spring, summer, autumn and winter) based on the recorded date. Seasonal summaries were produced both as overall totals and as species-level heatmaps to visualise intra-annual patterns of cave use. Cave-level patterns of mammal diversity were explored using the distribution of species richness across sites. Distances from cave entrances were analysed to quantify species-specific penetration into cave systems. Records lacking distance measurements were ex-

Table 1. Occurrence of non-volant mammals across surveyed caves in Bulgaria. For each taxon, we report the number of cave sites where it was detected (Sites) and independent detection events (Occurrences). Records include camera-trap events, bycatch pitfall trapping, direct observations, and tracks.

Order	Family	Species	Sites (n)	Independent detection events (Occurrences) (n)
Rodentia	Echimyidae	<i>Myocastor coypus</i>	1	2
	Gliridae	<i>Dryomys nitedula</i>	1	1
		<i>Glis glis</i>	7	107
	Cricetidae	<i>Microtus subterraneus</i>	1	1
	Muridae	<i>Apodemus cf. sylvaticus</i>	1	1
Eulipotyphla	Soricidae	<i>Crocidura suaveolens</i>	2	2
		<i>Neomys milleri</i>	3	11
Carnivora	Mustelidae	<i>Martes foina</i>	9	32
		<i>Meles meles</i>	4	5
		<i>Mustela putorius</i>	1	1
	Ursidae	<i>Ursus arctos</i>	2	10
	Canidae	<i>Vulpes vulpes</i>	4	7
	Felidae	<i>Felis silvestris</i>	3	4
Artiodactyla	Bovidae	<i>Rupicapra rupicapra balcanica</i>	1	31

cluded. Because depth distributions were strongly right-skewed, differences among species were tested using the Kruskal-Wallis rank-sum test. Pairwise contrasts were assessed using Dunn tests with Benjamini-Hochberg adjustment. Median and maximum penetration distances were calculated to distinguish typical from extreme cave use. The relationship between cave altitude and species richness was evaluated using ordinary least squares linear regression. Because richness data may deviate from parametric assumptions, the analysis was complemented with a non-parametric Spearman rank correlation. All statistical analyses and visualisations were conducted in R (R Core Team, version 4.1.1). Figures were produced using ggplot2 and patchwork (Wickham, 2016; Pedersen, 2025).

Results

The analysed data comprises 214 occurrences of non-volant mammals from 29 caves distributed across Bulgaria (Fig. 1). In total, 14 mammal taxa were documented (Table 1), representing Eulipotyphla

(Soricidae – 2 species), Rodentia (Muridae – 1 species, Cricetidae – 1 species, Echimyidae – 1 species, Gliridae – 2 species), Carnivora (Mustelidae – 3 species, Canidae – 1 species, Felidae – 1 species, Ursidae – 1 species) and Artiodactyla (Bovidae – 1 species). Records were unevenly distributed among caves and years, reflecting a combination of structured sampling and opportunistic observations.

The assemblage was dominated by a small number of taxa (Fig. 2A). No species had a wide distribution across all sampling sites. *Glis glis* accounted for the largest share of occurrences ($n = 107$), followed by *Martes foina* ($n = 32$) and *Rupicapra rupicapra balcanica* ($n = 31$; Table 1). However, relative record frequency did not correspond closely to spatial distribution (Fig. 2B). Although *R. r. balcanica* was frequently recorded, it was detected in only one cave regularly used by the species; its high number of records therefore reflects repeated detections at a small number of sites rather than a broad distribution across the cave system. In contrast, *M. foina* (31.03% of caves – 9 sites) and *G. glis* (24.13% – 7 sites) combined relatively high record frequencies with broader distribution across the surveyed cave system (cate-

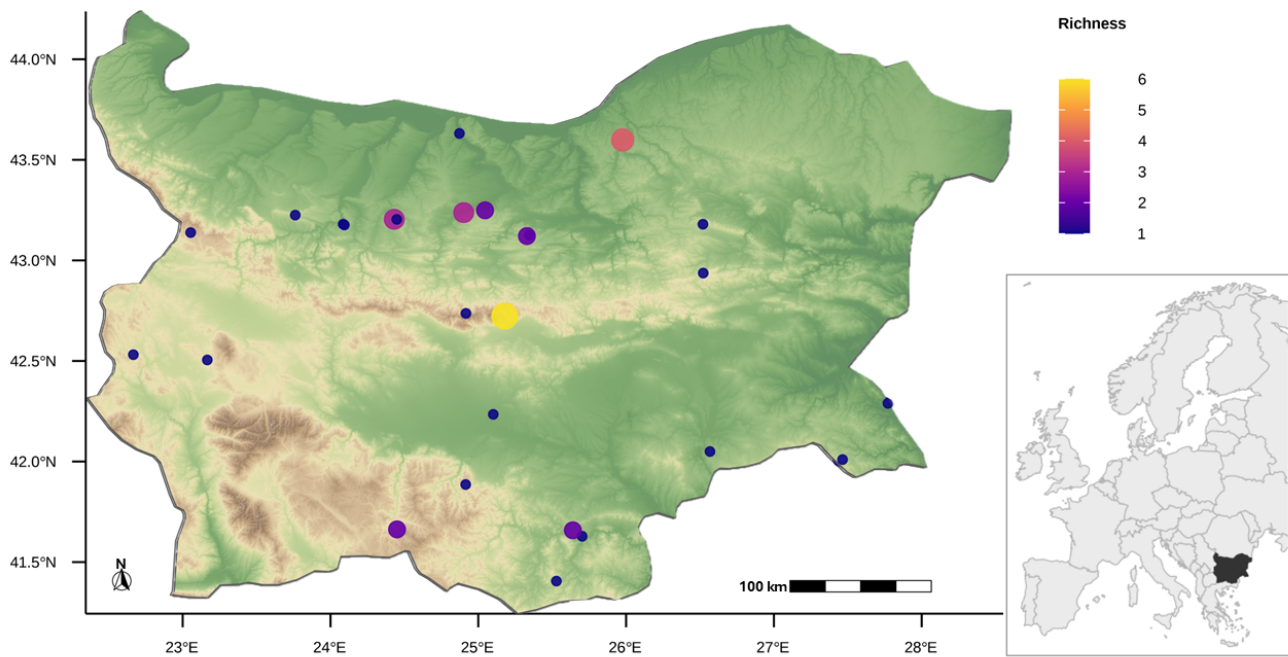


Fig. 1. Surveyed caves in Bulgaria. Circles indicate cave localities; size and colour correspond to mammal species richness recorded at each site.

gory common, 7–11 sites). On the other hand, *Meles meles* and *Vulpes vulpes* were recorded at only four sites (category rare). Most species showed low occupancy (category occasional, <3), typically occurring in fewer than 11% of caves, and many were recorded at a single site only (Fig. 2C). Small insectivores and rodents were detected predominantly by pitfall trapping, whereas medium- and large-sized mammals were recorded mainly through direct observations, camera trapping and indirect evidence such as scats. As records represent observation events rather than unique individuals, repeated detections of the same animals across sampling occasions cannot be excluded. The faunistic structure based on record frequency was strongly uneven (Fig. 2C). In contrast, the occupancy-based classification emphasised the restricted distribution of most species (Fig. 2C), with only a small number occurring across a larger proportion of caves.

Species richness per cave was generally low (Fig. 3A). Most caves harboured one or two taxa, and only a few sites supported richer assemblages. Mammal records were strongly concentrated near cave entrances (Fig. 3B), with only occasional deep penetrations. Depth differed significantly among

species (Kruskal-Wallis: $\chi^2 = 28.30$, $d.f. = 6$, $p = 8.24 \times 10^{-5}$). Although the deepest single record was obtained for *Martes foina* (600 m), *Neomys milleri* showed the greatest typical penetration (median 175 m), whereas most taxa remained concentrated near cave entrances. No significant relationship was detected between cave altitude and mammal species richness (Fig. 3C; linear model: $R^2 = 0.011$, $p = 0.603$; Spearman $\rho = -0.06$, $p = 0.765$; $n = 27$).

The temporal distribution of records shows a pronounced increase after 2020 (Fig. 4A), with earlier years characterised by sporadic observations, whereas more recent data reflect intensified survey effort. Seasonal patterns were also uneven: records with known seasons were concentrated in summer and autumn, whereas winter detections were scarce (Fig. 4B). The species-level heatmap highlights that this seasonal signal was driven largely by *Glis glis* and *Martes foina*, with most taxa recorded infrequently across seasons (Fig. 4C). Pitfall data indicate that small mammals were recorded mainly during the warmer part of the year; the taxa most frequently detected by pitfalls were *Neomys milleri*, *Crocidura suaveolens*, *Apodemus* cf. *sylvaticus* and *Microtus subterraneus*.

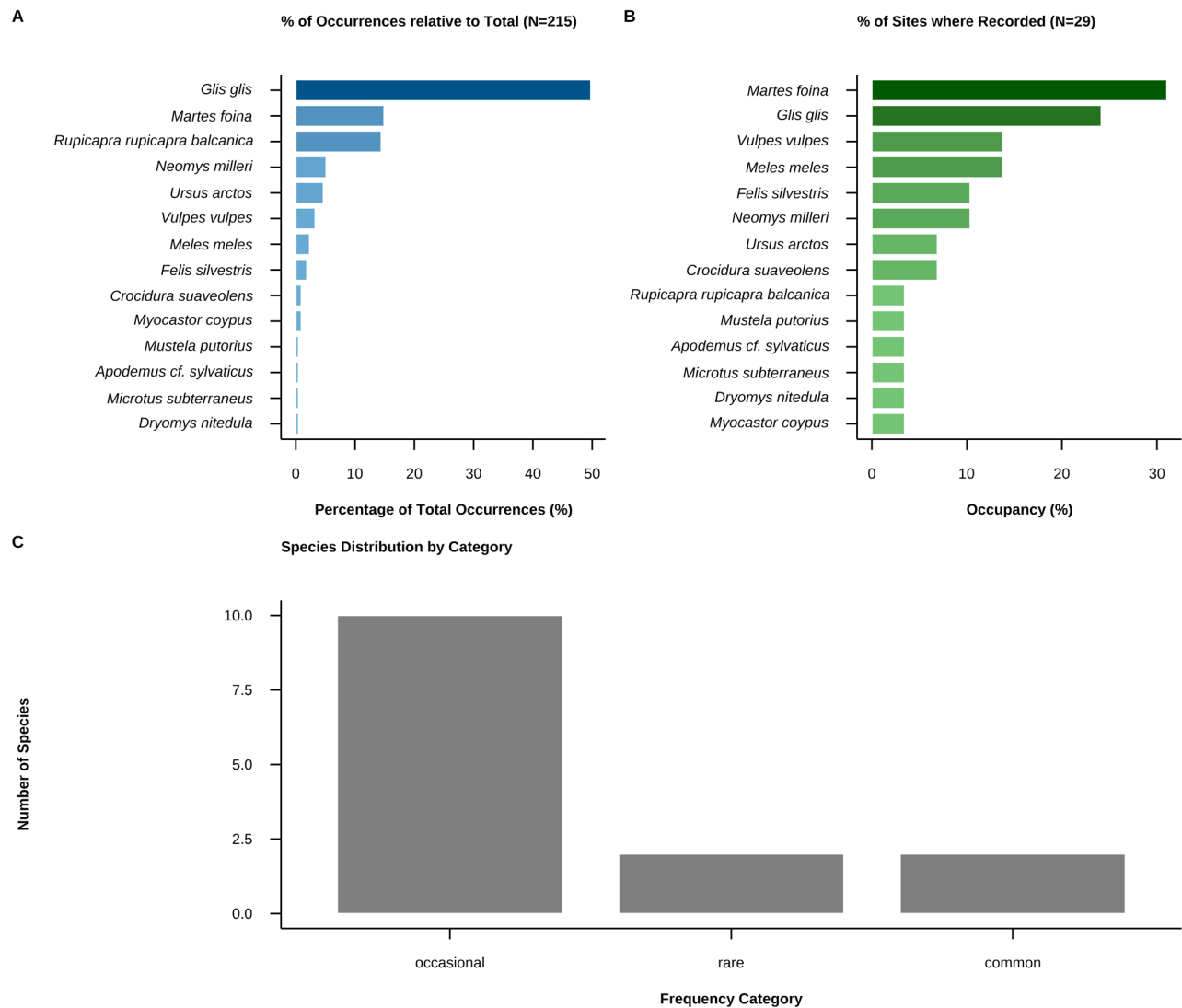


Fig. 2. Species contributions, occupancy and frequency structure. (A) Relative contribution of each species to the total number of independent occurrences (%). (B) Species occupancy expressed as the percentage of surveyed caves in which each species was detected (Occupancy %). (C) Occupancy-based frequency structure, showing the number of species assigned to categories reflecting spatial distribution (widespread, common, rare and occasional).

Discussion

The data assembled in this study demonstrate that caves in Bulgaria are used by a broader range of non-volant mammals than previously recognised (Beron, 2015), although the pattern of occurrence clearly indicates facultative rather than obligate subterranean use. Across the 29 investigated caves, records were obtained for 14 taxa representing orders Eulipotyphla, Rodentia, Carnivora and Artiodactyla. The highly uneven faunistic structure, with only a few frequently recorded species and many isolated observations, is

consistent with patterns observed in regional studies, where a small number of common mammals dominate cave use while most species occur sporadically, reflecting opportunistic rather than obligate subterranean use (Montalvo et al., 2017).

The assemblage is composed mainly of ecological generalists. Small insectivores, particularly *Neomys milleri* and *Crocidura suaveolens*, were recorded chiefly along subterranean watercourses and in dark entrance zones. Water shrews were detected up to ~400 m from cave entrances, usually following underground streams, indicating active exploitation

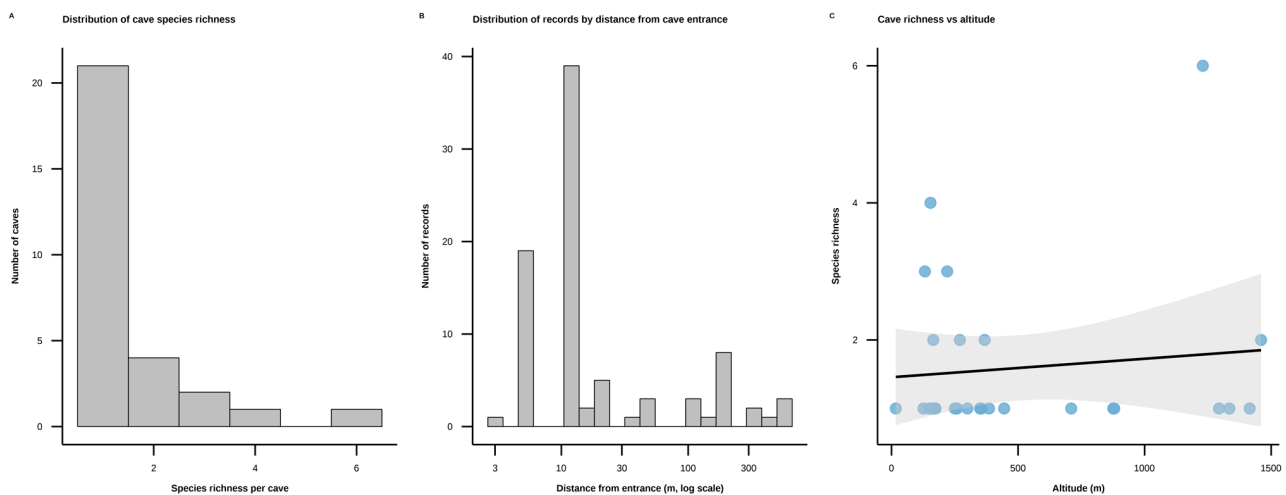


Fig. 3. Cave-level richness patterns. (A) Distribution of mammal species richness per cave. (B) Distribution of records by distance from cave entrance (log scale). (C) Relationship between cave altitude and mammal species richness (solid line, linear regression; shaded area, 95% confidence interval).

of aquatic corridors rather than accidental penetration. Medium-sized carnivores, especially *Martes foina*, appear to use caves primarily as temporary shelters, and several instances of bat predation were also documented during the survey. The stone marten predation on bats has been documented in previous studies (Nováková & Vohralík, 2017), however, our observations indicate repeated predation events within some important bat hibernacula, suggesting a consistent use of these sites as foraging grounds. In our study, the edible dormouse (*Glis glis*) was also recorded in caves (Fig. 5B), supporting previous findings that this species uses underground sites not only for hibernation but also as regular shelters during the active season (Marchewka & Postawa, 2022). In Italy, *Glis glis* was recorded breeding in caves, usually near the entrance, approximately 20–30 m (Scavelli & Bassi, 1995). In our dataset, seasonal patterns were strongly biased towards the warmer part of the year. This likely reflects both biological activity and sampling effects, as pitfall efficiency and small-mammal activity decline markedly in winter. The cave assemblage largely mirrors the surrounding terrestrial fauna, reinforcing the interpretation that caves are used opportunistically rather than supporting a distinct mammal community.

Large mammals such as *Ursus arctos* were recorded only sporadically in the surveyed caves, suggesting that these sites are used primarily as an

occasional refuge, rather than regular denning habitats. Published sources indicate that brown bears in Bulgaria may establish maternity dens in shallow caves in remote high-elevation forest and subalpine zones (typically above 1000–1800 m a.s.l., usually small (c. 2–3 m deep) and lined with plant material (Popov et al., 2007). The apparent scarcity of cave records should, however, be interpreted with caution. Precise locations of bear dens are commonly withheld in the literature for conservation reasons, and the present study follows the same approach. Consequently, the low number of documented occurrences likely reflects reporting constraints rather than genuinely rare cave use by *U. arctos* in the country. Furthermore, in one case, a camera trap was initially deployed to monitor potential hibernation activity of *Ursus arctos*. However, it was removed after chamois (*Rupicapra rupicapra*) were recorded using the cave, as field observations suggest that bears do not hibernate in caves regularly used by chamois (unpublished data).

The occurrence of mammals in caves reflects both incidental incursions and the repeated use of suitable subterranean habitats. The present results indicate that trophic resources are a key determinant of these patterns. Subterranean streams sustain aquatic invertebrates, whereas bat colonies provide concentrated inputs of organic matter, such as guano and carcasses, creating resource-rich patches within otherwise nutrient-limited systems. Observations from several caves

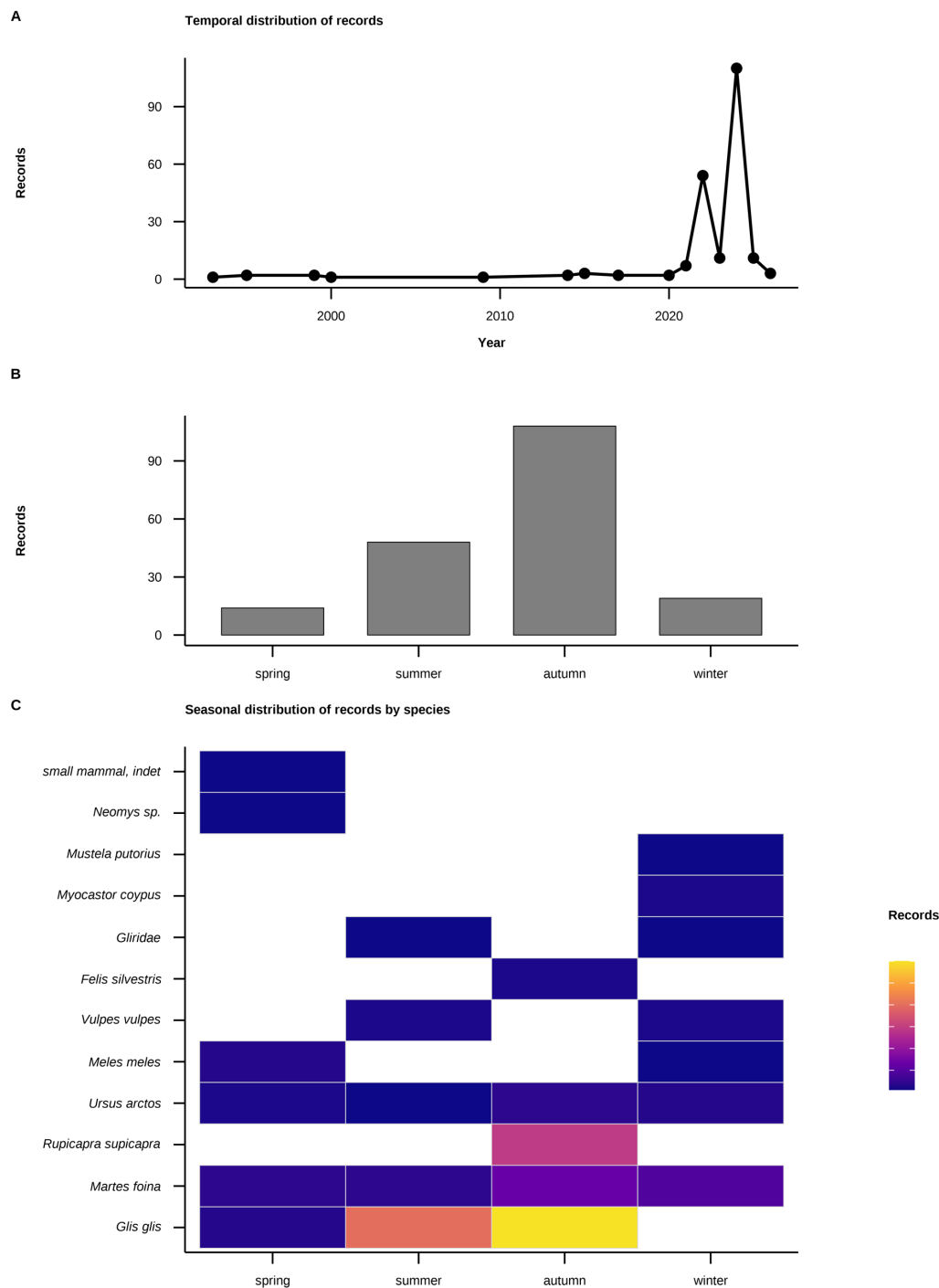


Fig. 4. Temporal and seasonal distribution of records. (A) Records per year (1993–2026), illustrating the increase in survey effort over time. (B) Seasonal totals for records with known seasons. (C) Seasonal distribution of records by species (heatmap), based on observations with known seasons.

show that bat remains beneath hibernating colonies are rapidly removed, most plausibly by carnivores such as martens (Fig. 5A), polecats and wild cats. Mammalian predation on bats has been documented

previously for a range of taxa, including *Martes foina*, *Vulpes vulpes* and *Apodemus sylvaticus* (Bekker, 1989; Romanowski & Lesiński, 1991; Kokurewicz, 2004; Haarsma & Kaal, 2016). In particular, detailed

monitoring of Dutch hibernacula has shown that predation by wood mice may be systematic and can influence local bat populations (Haarsma & Kaal, 2016). Given that Bulgaria supports some of the largest bat aggregations in Europe (Toshkova & Simov, 2025), comparable predator–prey interactions are likely, although they remain poorly documented. Direct observations are scarce; however, occasional records suggest that predation events may be locally intense. A notable example is the mass predation of bats by a domestic or feral cat in a tourist part of the Orlova Chuka Cave in 1996 (Fig. 5C), indicating that episodic events can result in substantial mortality within hibernating colonies. There is currently no evidence for rat predation on bats in Bulgarian caves, despite recent reports from urban hibernacula elsewhere in Europe (Gloza-Rausch et al., 2025). This absence may reflect limited observation rather than true absence. The systematic documentation of such interactions is increasingly important. Predator–prey contacts involving bats may create opportunities for cross-species pathogen transmission, particularly where carcasses accumulate or are handled by multiple scavengers. Bats are recognised reservoirs for a range of zoonotic agents (Calisher et al., 2006; Brook & Dobson, 2015), and increased contact between bats and other mammals and humans may elevate transmission risk (Salinas-Ramos et al., 2021; Gloza-Rausch et al., 2025). Improved documentation of predation events, carcass persistence and scavenger assemblages is therefore essential for understanding both ecological dynamics and potential public health implications.

Furthermore, although mammalian use of caves is often sporadic, its ecological effects may be disproportionate. Large mammals can introduce substantial allochthonous organic matter, while predators and scavengers redistribute biomass through carcass removal. Such processes are likely to influence nutrient availability and microhabitat conditions at fine spatial scales, with potential consequences for the cave ecosystem functioning. In this context, particular attention should be given to the documented use of caves in Bulgaria by invasive alien mammals such as the nutria (Fig. 5D), whose rapid range expansion and population growth in recently invaded regions may pose an additional threat to subterranean habitats.

Whether any non-volant mammal can complete its entire life cycle within a cave environment remains

uncertain. However, the repeated occurrence of water shrews deep within cave systems suggests the possibility of prolonged subterranean activity associated with underground streams and food resources. Soil traps placed in cave passages, particularly beneath or near bat colonies, contained large numbers of invertebrates, including moths and flies, including their larvae, as well as beetles such as Tenebrionidae and predatory Staphylinidae and Carabidae. Rove beetles (Staphylinidae) were particularly numerous in some caves, such as Parnitsite and Devetashka. The abundance of these potential prey items suggests that cave environments may provide substantial food resources, and water shrews may enter subterranean habitats in response to concentrations of invertebrates. Diet studies show that although water shrews are semi-aquatic, they consume predominantly terrestrial prey, with aquatic organisms forming a smaller proportion of the diet, indicating considerable flexibility in prey use (Churchfield & Rychlik, 2006).

Furthermore, although data on the home range of *Neomys milleri* are lacking, radio-tracking studies of the larger and closely related species *Neomys fodiens* indicate relatively small home ranges, averaging about 207 m² in spring–summer and around 106 m² in autumn–winter, with activity largely confined to stream habitats (Lardet, 1988). Such spatially restricted ranges suggest that short sections of subterranean watercourses could potentially sustain individuals for extended periods if suitable prey is available. Although this does not demonstrate a fully subterranean life cycle, it raises the possibility that water shrews may spend substantial portions of their lives within cave-stream environments, particularly where invertebrate prey is abundant. Evaluating this hypothesis will require targeted long-term studies and more detailed investigation of aquatic cave habitats using specialised survey methods, as these species remain difficult to observe and are consequently poorly documented in subterranean ecosystems.

The findings also have practical implications. Bulgaria hosts more than 100 caves and mines recognised as important underground bat roosts of national or international significance (Ivanova, 2005; Deleva et al., 2023). Such sites represent predictable concentrations of resources that may attract a range of terrestrial mammals. However, cave monitoring in Bulgaria has traditionally focused on bats, yet the present results show that a broader spectrum of vertebrates regularly uses these habitats. Incorporating non-volant



Fig. 5. Different mammals in the caves: A – Stone marten in the Urushka Maara Cave; B – Edible dormouse in the Popov Izvor Cave; C – Mass predation on bats in the tourist cave Orlova Chuka in 1996. Numerous bat carcasses and detached wings on the cave floor following repeated predation by a domestic or feral cat. This observation illustrates the potential for localised, high-intensity predation events within hibernating colonies; D – Nutria entering one of the entrances of the Chirpan Bunar Cave.

mammals into monitoring protocols could improve the ecological interpretation of bat mortality by providing insight into predator–scavenger interactions. An integrated monitoring approach would also help address persistent knowledge gaps regarding the role of non-volant mammals in cave ecosystems and their interactions with bat colonies in Bulgaria (Toshkova & Simov, 2026).

The close correspondence between the modern cave-visiting fauna documented here and the vertebrate assemblages reported from Bulgarian cave deposits (Beron, 2006) suggests that part of the fossil record may reflect the direct use of caves by surface-dwelling species. Cave assemblages are commonly interpreted as the result of multiple taphonomic processes, with predator activity, particularly owl-

mediated accumulation at cave entrances often considered dominant. However, the present observations show that a range of small-bodied taxa (e.g. *Glis glis*, *Crocidura suaveolens*, *Neomys* spp., *Apodemus* cf. *sylvaticus*, *Microtus subterraneus*) actively enter and utilise caves. Remains of *Rupicapra rupicapra*, frequently reported from Quaternary cave deposits across Europe (Fosse et al., 2020), may similarly reflect natural use of karstic cavities, as indicated by repeated records of *R. r. balcanica* in the studied sites. Taken together, this shows that modern ecological data provide a robust framework for interpreting fossil cave assemblages. Considering direct cave use alongside predator-mediated accumulation allows a more accurate reconstruction of the processes responsible for vertebrate deposition in karst environments.

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Conflicts of interest

No potential conflict of interest has been reported by the authors, reviewers, or subject editor. As members of the editorial board, Mario Langourov, Ilya Acosta-Pankov and Nikolay Simov withdrew from discussions and decisions on the manuscript.

Author’ contributions

(using [CrediT](#) )

Nia Toshkova: conceptualisation, data curation, formal analysis, investigation, methodology, software, visualisation, writing—original draft, writing—review and editing; Vladimir Todorov: data curation, formal analysis, investigation, methodology, software,

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Supplementary materials

01

Document title: An Excel dataset compiling all recorded occurrences of non-volant mammals included in this study, encompassing 214 records of 17 taxa from 29 caves in Bulgaria (1993–2026), with associated metadata on locality, detection method, and cave zone.

Kind of document: Microsoft Excel (OpenXML)

MIME type: application/vnd.openxmlformats-officedocument.spreadsheetml.sheet

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