Article

Not peer-reviewed version

Notes on the Winter Bat Mortality in Bulgaria and the Demographic Structure of Deceased Individuals from One of Europe's Largest Bat Colonies

Nia Toshkova * and Nikolay Simov

Posted Date: 15 October 2025

doi: 10.20944/preprints202510.0852.v1

Keywords: bats; winter mortality; hibernation; age

Preprints.org (www.preprints.org) | NOT PEER-REVIEWED | Posted: 15 October 2025 doi:10.20944/preprints202510.0852.v1

Article

Notes on the Winter Bat Mortality in Bulgaria and the Demographic Structure of Deceased Individuals from One of Europe's Largest Bat Colonies

Nia Toshkova * and Nikolay Simov

National Museum of Natural History, Bulgarian Academy of Sciences, 1 Tsar Osvoboditel Blvd,
1000 Sofia, Bulgaria
* Correspondence: niyatoshkova@gmail.com

Abstract

Understanding the drivers of population dynamics in long-lived, K-selected species such as bats is critical for conservation, particularly during vulnerable life-history stages like hibernation. We reviewed winter mortality records from more than 109 monitored hibernacula in Bulgaria. We found that significant die-offs (>30 individuals from at least three species) were recorded at only three sites, suggesting that such events are rare but potentially consequential for local populations. To reveal how habitat use shapes vulnerability during winter, we investigated hibernation preferences of cave-dwelling bats in Bulgaria. We further analysed the age structure of deceased *Miniopterus schreibersii* (Bonaparte, 1837) from Bulgaria's largest hibernation colony following mortality events in winter 2022. Carcasses spanned a wide range of age classes, yet younger individuals predominated, consistent with the idea that early-life mortality represents a key demographic filter in bats. These findings emphasise the need for consistent mortality monitoring in bats, using standardised protocols that account for detection biases, scavenger removal, and site-specific variation. Such efforts are essential for clarifying the roles of environmental extremes, disease, and human disturbance in winter mortality.

Keywords: bats; winter mortality; hibernation; age

1. Introduction

Understanding patterns of wildlife survival is fundamental to both population ecology and conservation. However, for many species, particularly bats, obtaining reliable survival estimates is challenging due to both biological and logistical constraints [1]. Bats are nocturnal, roost in concealed or inaccessible locations, and have relatively long lifespans and low reproductive rates, necessitating long-term studies to detect demographic trends. Traditional approaches, such as the Capture–Mark–Recapture method, provide valuable estimates but are often limited by low recapture rates, mark loss, and the need for long-term data [2].

As an alternative, direct observations of mortality events can provide critical—albeit episodic—insight into population-level mortality and stressors, especially during biologically sensitive periods, such as reproduction and hibernation. While mortality records alone cannot provide formal survival estimates, they are particularly valuable in identifying acute threats and their demographic consequences. The emergence of White-nose Disease (WND) in 2006 demonstrated the importance of mortality surveillance, with the fungal pathogen driving unprecedented die-offs among hibernating bats in North America [3]. Since then, monitoring efforts have increasingly focused on detecting mortality events during hibernation, when bats are in a physiologically vulnerable state and may be disproportionately impacted by disease and environmental stressors [4].

A comprehensive assessment of such mortality events requires not only documentation of fatalities but also an investigation into their underlying causes and demographic impacts [5]. In

doi:10.20944/preprints202510.0852.v1

particular, understanding which age classes are most affected is essential for interpreting population-level consequences. Age-specific mortality can influence recruitment rates, recovery potential, and long-term viability [6]. Incremental dentine layer analysis has emerged as a robust method for age estimation, with a clear distinction between first-year individuals and adults, making it particularly suited to assessing whether juveniles face higher winter mortality [7–9].

Here, we address the gap in knowledge on winter bat mortality by compiling records from hibernation surveys across Bulgaria. Focusing on unusual mortality events (UMEs) [4], we assess their frequency, distribution, and demographic composition. Additionally, we investigate how hibernation preferences—specifically, altitude and roost temperature—may be related to mortality risk. We further analyse the age structure of deceased *Miniopterus schreibersii* from Bulgaria's largest hibernation colony, using dentine layer analysis to test whether mortality disproportionately affects younger individuals. We aim to provide new insight into the demographic consequences of winter mortality and to highlight the need for systematic surveillance to inform bat conservation.

2. Materials and Methods

2.1. Hibernacula survey

We analysed winter roost monitoring records from the dataset "Bat occurrences from Bulgaria" [10], which is openly available via the Global Biodiversity Information Facility (GBIF). The dataset compiles observations from the National Biodiversity Monitoring System of Bulgaria (2003–2023), coordinated by the Ministry of Environment and Water, together with earlier survey efforts dating back to 1991. Monitoring was carried out annually between 1 December and 31 March, most frequently in February when colony sizes peak.

During each survey, observers recorded species composition, colony size, environmental parameters (temperature, humidity), evidence of disturbance, and carcass counts. These environmental variables were also used to characterise species-specific hibernacula preferences across sites. Carcasses were identified in the field based on external morphology [11]. Although unusual mortality events (UMEs; > 7 individuals) [4] were noted, their systematic recording was inconsistent across years and sites.

Across the 30-year monitoring period, more than 109 hibernacula were visited (Figure 1). Survey frequency varied by site: priority caves such as Devetashka, Parnicite, and Ivanova Voda were visited almost annually—some years more than once—while smaller or less accessible sites were surveyed less regularly, often at intervals of two to three years (Table 1). This variation in survey frequency should be taken into account when interpreting the occurrence and apparent rarity of mortality events. Data management and statistical analyses were performed in R (version 4.1.1) [12].

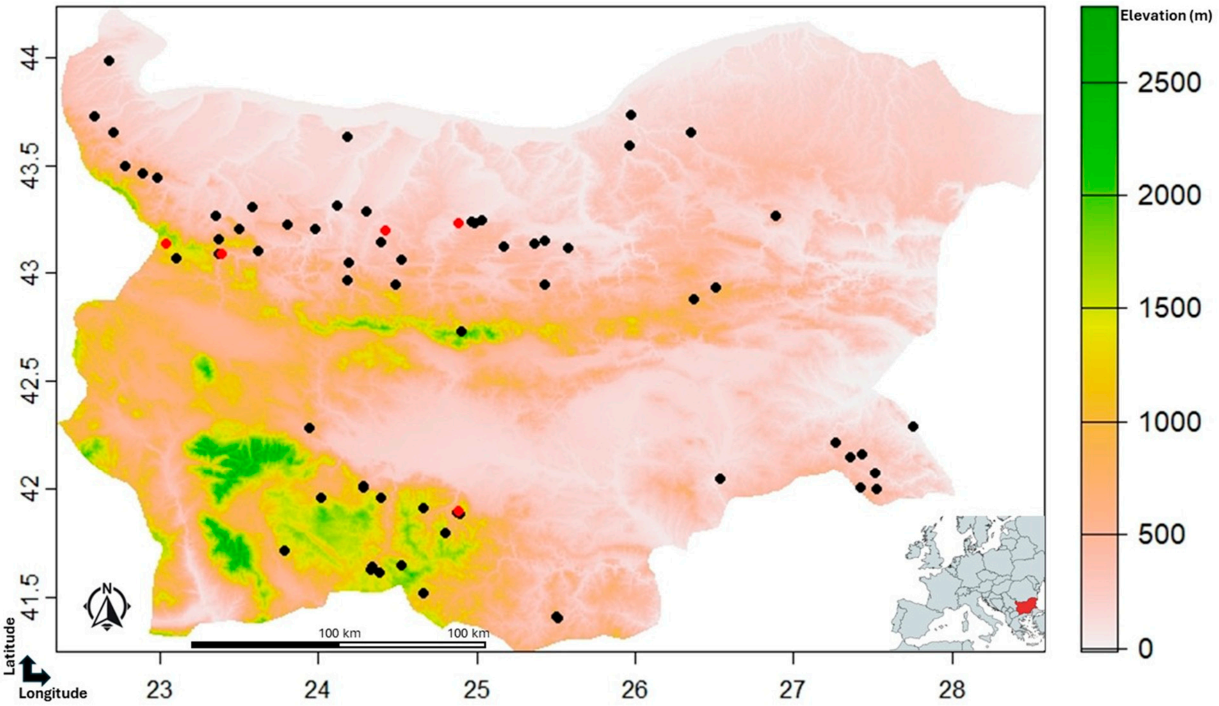

Figure 1. Geographic locations of the important hibernacula in Bulgaria (black dots), with sites where mortality was most often recorded highlighted in red.

Table 1. Survey effort at the Bulgarian hibernacula where mortality events have been reported. Numbers indicate the total visits per site and the years during which surveys were conducted.

Site	Total visits	Years covered	Notes (e.g. multiple visits per year)
Devetashka	14	1997–2024	Several years with >1 visit
Parnicite (Dolen parnik)	14	1996–2023	Several years with >1 visit
Ivanova Voda	6	1997–2022	Surveyed every 2–3 years
Orlova Chuka	12	1991–2022	Several years with >1 visit
Pavla (Ravnogorskata Peshtera)	4	2008–2014	Occasional surveys
Skoka	2	2008–2016	Occasional surveys
Ponora	7	2012–2022	Surveyed every 2–3 years

2.2. Bat sampling

Our demographic analysis focused on *Miniopterus schreibersii*, an insectivorous and cave-dwelling bat. The species is highly dependent on subterranean roosts, primarily occupying caves and abandoned mine galleries throughout the year. Adults weigh 10–18 g, yet the species is unusually long-lived for its size and individuals are known to reach 22 years in the wild (AnAge database). Long-term mark–recapture studies in Bulgaria confirm survival beyond 12 years (NMNH-BAS dataset). In Bulgaria, *M. schreibersii* forms some of the largest winter colonies across its range. Several roosting sites are easily accessible, facilitating both the observation and collection of deceased individuals. All samples for this study were collected at the end of the hibernation period during the winter of 2022 from Parnicite (Dolen Parnik) Cave (N43°20′, E24°41′, altitude 232 m), which hosts an estimated 53,468 individuals of the target species in a mixed-species colony. The tunnel-shaped system extends 2.5 km, with continuous water flow and two entrances. Colonies occupy a section near the exit, where slower water forms small pools. At the end of the hibernation period in February and March 2022, 40 carcasses were collected from the water surface and stored at –20 °C. From each individual, the upper canine tooth was extracted using metal tweezers under 10× magnification using a Carl Zeiss STEMI 2000 stereomicroscope. The material is preserved in the collection of the National

Museum of Natural History, Sofia, Bulgaria (NMNHS). Carcases were collected under a permit issued by the Bulgarian Biodiversity Act (No 830/19.09.2020).

2.3. Laboratory processing and age determination

The age of adult individuals was determined using cross-sections of the upper canine tooth. The growth layers in the dentine exhibited a complex structure, with the primary element appearing as an intensely stained line of varying width, representing one full year of life [7,8,13–15]. A total of 34 individual samples of dead *Miniopterus schreibersii* were analysed.

Samples (upper canines) were fixed and stored in neutral buffered formalin for several months, washed twice with phosphate buffer containing Triton™ X-100 (0.3%), decalcified in EDTA 0.15 M for 10–14 days, rinsed, dehydrated through graded ethanol, cleared in xylene, embedded in Paraplast Plus®, sectioned at 15 µm, and stained with haematoxylin and eosin (H&E). Age estimation was conducted by counting dentine rings in the cross-sections (Figure 2), with ring counts performed independently by three researchers. Final age assignments were based on a consensus estimate derived from the counts. The samples were examined and photographed using an Amplival (Carl Zeiss Jena) microscope under brightfield conditions with an EOS 2000D (Canon) camera attached. Multiple images were stacked with Helicon Focus (Helicon Soft) to improve focus.

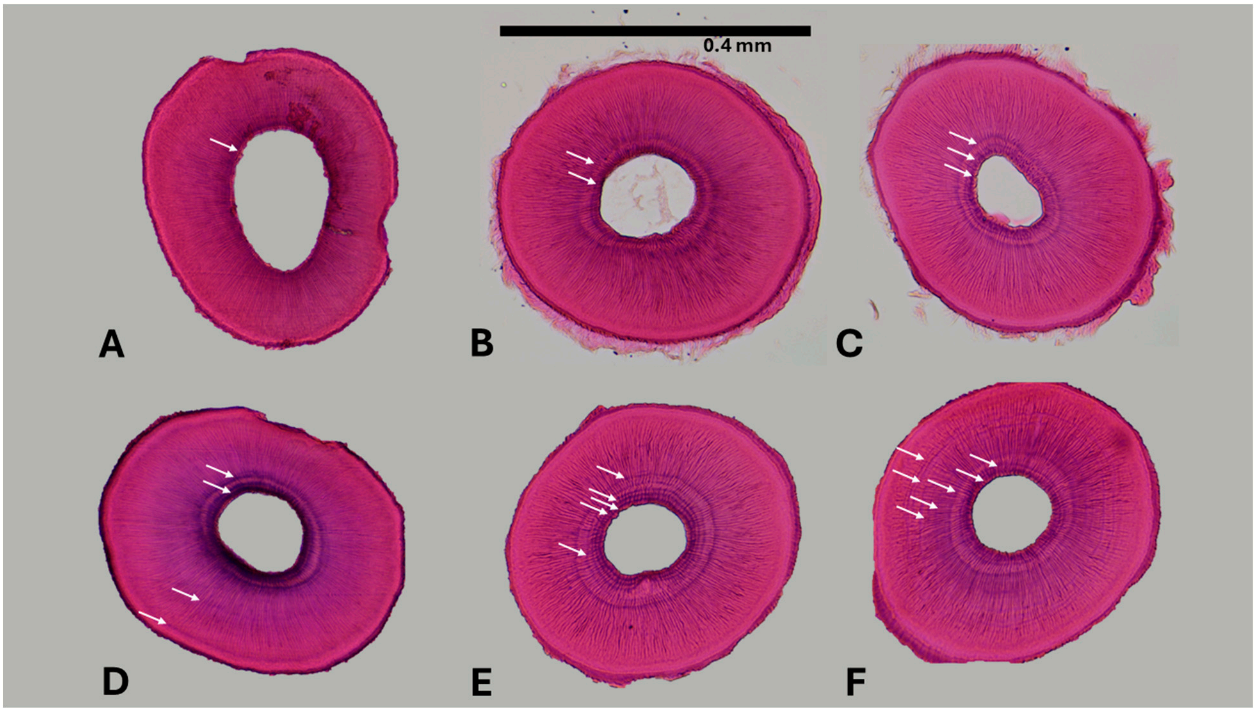

Figure 2. Cross-sections of upper canines from *Miniopterus schreibersii*. White arrows indicate dentine growth layers used for age estimation. Panels A–F illustrate examples from different age classes.

3. Results

Winter mortality was recorded across seven bat species at nine hibernation sites in Bulgaria (Figure 3; Table 2). The majority of unusual mortality events (UMEs) were concentrated in winter 2012, with additional events documented in later years at fewer sites. Mortality was unevenly distributed, both taxonomically and geographically: Miniopterus schreibersii accounted for the largest and most recurrent losses, particularly in Devetashka and Parnicite caves, whereas Myotis capaccinii and M. myotis/blythii experienced substantial mortality at Ivanova Voda during the same winter. In contrast, Rhinolophus euryale and R. ferrumequinum were only sporadically affected, with small numbers scattered across sites and years. Taken together, these findings indicate that

doi:10.20944/preprints202510.0852.v1

winter mortality was highly species- and site-specific, with M. schreibersii experiencing the most frequent and severe losses.

Table 2. Summary of winter bat mortality events recorded at Bulgarian hibernacula (2012–2023), showing affected sites, species, year of occurrence, and number of deseased individuals (n).

Site	Species	Year	n
Devetashka Cave	*Miniopterus schreibersii*	2012	75
Ivanova Voda	*Myotis capaccinii*	2012	37
Ivanova Voda	*Myotis myotis/blythii*	2012	65
Parnicite Cave	*Miniopterus schreibersii*	2012	15
Parnicite Cave	*Miniopterus schreibersii*	2022	40
Pavla	*Miniopterus schreibersii*	2014	2
Skoka Cave	*Miniopterus schreibersii*	2012	6
Parasinskata Propast	*Rhinolophus euryale*	2012	8
Ponora	*Rhinolophus euryale*	2012	6
Orlova Chuka	*Rhinolophus euryale*	2021-2022	5
Morovitsa	*Rhinolophus euryale*	2023	1
Parnicite Cave	*Rhinolophus ferrumequinum*	2012	8

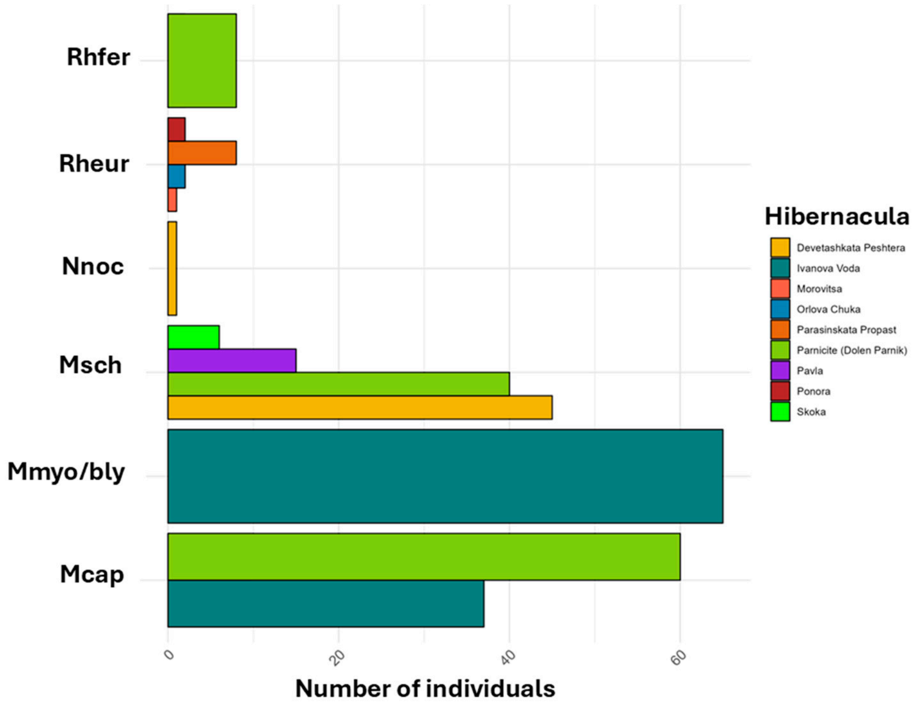

Figure 3. Winter mortality events in hibernating bats across Bulgaria (2003–2023). Events were recorded in seven species or species groups, with unusual mortality events (UMEs, >7 carcasses) documented at four sites.

Abbreviations: Nnoc = *Nyctalus noctula*; Msch = *Miniopterus schreibersii*; Mcap = *Myotis capaccinii*; Mmyo/bly = *Myotis myotis/blythii*; Rheur = *R. euryale*; Rhfer = *R. ferrumequinum*.

Across Bulgaria, species exhibited distinct preferences for hibernacula (Figure 4). Most bats selected humid caves at lower altitudes, whereas others occupied colder, high-elevation roosts. These patterns suggest that wet and stable microclimates are generally favoured for hibernation.

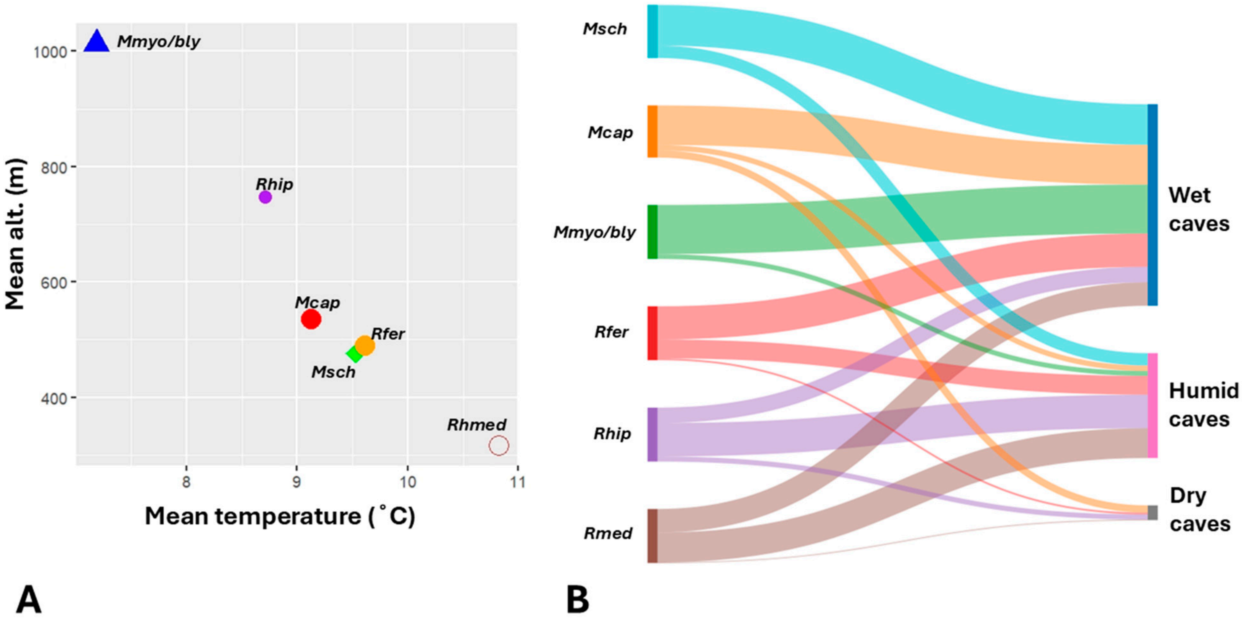

Figure 4. Hibernacula preferences of Bulgarian bat species. Bars indicate mean roost temperature, altitude, and humidity type. Most species were associated with wet, humid caves, while some occurred at colder, high-altitude sites. Rhip = *Nyctalus noctula*; Msch = *Miniopterus schreibersii*; Mcap = *Myotis capaccinii*; Mmyo/bly = *Myotis myotis/blythii*; Rhmed = *R. media*; Rfer = *R. ferrumequinum*.

The 34 *M. schreibersii* individuals aged from Parnicite Cave spanned 0–7 years, but the distribution was skewed towards younger bats (Figure 5). The modal mortality age was 3 years, with a mean of 2.68 ± 1.63 years (SD).

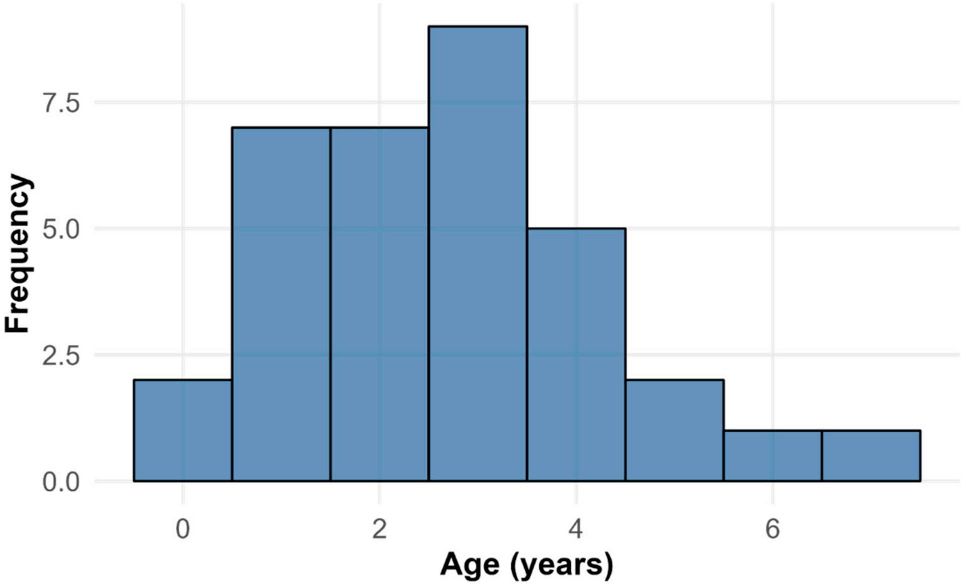

Figure 5. Age distribution of *Miniopterus schreibersii* carcasses from Parnicite Cave (n = 34). Ages ranged from <1 to 7 years, with a mode of 3 years and mean ± SD = 2.68 ± 1.63.

4. Discussion

In this study, we analysed records of winter mortality from bat hibernacula in Bulgaria. Mass die-offs, defined here as events exceeding 30 individuals, were recorded at only three of the (>40) important underground habitats that are regularly surveyed [16,17]. Although uncommon, such events may affect local populations and should not be dismissed as anomalies. Their apparent scarcity may reflect both a true low incidence and substantial under-reporting, owing to inconsistent monitoring protocols and the rapid removal of carcasses by scavengers or floods within roosts.

Early bat research in Bulgaria focused mainly on colony assessments and the protection of underground roosts [18], with systematic recording of mortality events emerging only later. However, historical evidence supports the view that winter mortality events were under-documented prior to the onset of regular monitoring. Unsystematic field observations from Ivanova Voda and Parnicite cave describe dead bats observed during the winters of 1994–1995 and 1999–2000 (S. Delchev, in litt.). In Devetashka Cave, at least ten carcasses were recorded in the river and skeletal remains were found beneath or around the colony before 2003 (N. Simov, pers. obs.). During a subsequent visit to Ivanova Voda after 2003, additional carcasses were seen floating in the cave lake (N. Simov, pers. obs.). Although these records lack systematic quantification, they indicate that sporadic mortality events likely occurred earlier than documented, suggesting that such incidents may long have formed part of the natural or environmental stress regime affecting bat colonies.

The mortality events documented here appeared associated with colony size; however, previous models of UMEs indicate that size alone is not a reliable predictor of risk [4]. Environmental extremes are more likely to account for sudden die-offs. For example, the winter of 2012 was marked by prolonged cold snaps, coinciding with elevated mortality in our dataset. Similar effects were reported across Europe in 2010/11, when mortality in *Myotis bechsteinii* increased twelvefold and severe declines of *Myotis nattereri* populations were observed in the Netherlands, Belgium, and Poland, implicating continent-wide weather extremes as the driver [19]. In some parts of Europe, certain bat species have ceased storing fat for winter, leaving them particularly vulnerable to cold snaps [20]. However, recent evidence suggests that some species, including *Miniopterus schreibersii*, are actively foraging outside hibernacula during winter as a potential compensatory strategy to offset energy deficits [21,22]. Yet the degree to which prolonged cold snaps constrain this behaviour and affect population viability remains uncertain. Even though hibernation is a vulnerable period, modelling studies suggest that extended hibernation may enhance bat longevity [23], but empirical evidence linking hibernation duration to mortality risk remains limited and warrants further investigation.

Carcass preservation strongly influences how mortality is recorded in the field. In Devetashka Cave, carcasses are rapidly decomposed by amphipods (e.g., *Gammarus pulex cognominus* and *Niphargus bureschi*) or scavenged by shrews, whereas in Ivanova Voda they often persist afloat for extended periods. By contrast, bloated carcasses may persist at the surface into spring in some sites (e.g., Parnicite) but sink more rapidly in others. These differences between rivers and lakes underscore how habitat type and post-mortem processes can bias detection, complicating cross-site comparisons. Scavenger activity not only obscures mortality estimates but may also constitute an overlooked pathway for pathogen transmission [24,25], highlighting the importance of incorporating scavenger dynamics into future mortality assessments. In particular, mammals that enter bat caves may contribute to both carcass removal and pathogen circulation within these environments. Nevertheless, systematic data on their presence and behaviour in Bulgaria are still lacking.

A major challenge is the lack of systematic protocols for documenting winter mortality. Historically, such events were often considered part of the "normal" losses in large colonies and therefore went unrecorded. In many monitoring schemes, the extent of carcass collection was not explicitly reported, limiting the reliability of quantitative inference. The sporadic occurrence of mortality events further reduces the likelihood of detection. Addressing these gaps will require coordinated, standardised approaches, including regular surveys of key hibernacula, systematic carcass recovery, and the use of established post-mortem and necropsy protocols to distinguish environmental from disease-related causes of death [26–28]. Novel techniques, such as dental wear analysis, may provide additional insight into age structure, although their utility remains constrained by sparse comparative datasets [29].

Species-specific differences in hibernacula use may also influence both vulnerability to winter mortality and the likelihood of carcass detection. In our dataset, most bats were associated with wet, humid caves at lower altitudes, whereas others occupied colder, high-elevation roosts. Such preferences likely reflect trade-offs between energetic demands and microclimatic stability during hibernation. Colonies in more variable and unfavourable environments may face greater risks from extreme winters (e.g., Ivanova Voda), while those in more stable roosts may benefit from reduced energetic costs [10]. However, mortality still occurs in such sites, as observed at Parnicite, although detection can be biased as those sites are surveyed more often. Roost characteristics should therefore be evaluated not only as potential refuges but also in terms of how they influence the visibility of mortality events.

The use of incremental dentine and cementum lines to estimate the age of bats is subject to considerable uncertainty. Line clarity varies among species, counts may differ between teeth or sections, and external factors such as mechanical stress can generate non-annual increments [30,13]. In older individuals, rings may merge or become obscured, limiting the accuracy of age estimates at advanced stages [31]. In some taxa, multiple layers may form within a single year [32], while in other cases, counts may underestimate known ages [13]. Recent advances in epigenetics offer a promising alternative. The development of bat methylation clocks now allows hypotheses about age-related survival to be tested directly [33]. Epigenetic profiling provides accurate age estimates and has been linked to variation in mortality risk across sexes and social groups [34]. Moreover, methylation clocks supply an independent benchmark for evaluating tooth-based ageing methods, which remain largely unvalidated and subject to significant uncertainty. Thus, while the method used provides useful insights, it cannot yield precise chronological ages. However, the use of age classes neutralises this drawback and makes the technique suitable for the study.

The age structure of deceased *Miniopterus schreibersii* from Bulgaria's largest hibernation colony revealed individuals spanning a wide range of classes, though younger bats appeared predominant. Interpretation of this pattern is uncertain, however, as the colony's true age distribution remains unknown and reliable data on local longevity in the wild are lacking. One possibility is that younger bats dominate simply because they constitute the most common demographic, or plausibly because adults that survive the early years exhibit relatively high persistence. Capture–recapture studies of *Pipistrellus pipistrellus* support the latter view, showing juvenile survival to be approximately 20–25% lower than that of adults, both before and after hibernation [35]. Similarly, *Myotis bechsteinii* exhibits negligible senescence, with survival and reproduction remaining stable even into advanced age; mortality in this species appears to be driven primarily by episodic severe winters rather than intrinsic ageing [19]. Collectively, these findings suggest that early-life mortality is a critical demographic filter in long-lived bats.

5. Conclusions

This study offers only a snapshot of winter mortality in Bulgarian bat populations, but it underscores the broader need for refined census procedures. Even relatively small-scale mortality, if systematically recorded, may reveal long-term trends and emerging risks that currently go unnoticed. Understanding how age structure, environmental variation, and disease dynamics interact to shape mortality will be critical for predicting population resilience. Robust mortality surveillance and accurate age determination, strengthened by molecular tools such as epigenetic clocks, will be essential for understanding demographic processes and ensuring the conservation of bat populations across Europe.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org, Table S1: **Raw_data_dentine_growth_layers_Mschreibersii**. Each sample was independently examined by three observers (Nikolay, Nia, and Boyan). The number of visible dentine growth layers ("rings") was recorded and used for age estimation. The final age represents a consensus or averaged value among observers. Remarks indicate sample condition, missing structures, or discrepancies in counts.

Funding: This study was supported by the Bulgarian National Science Fund, project КП-06-Н51/9 ''Caves as a reservoir for novel and reoccurring zoonoses – ecological monitoring and metagenomic analysis in real time.''.

Institutional Review Board Statement: The bat survey was conducted following all relevant ethical guidelines to ensure minimal disturbance to the animals and their environment. Carcases were collected under a permit issued by the Bulgarian Biodiversity Act (No 830/19.09.2020).

Data Availability Statement: Raw survey data can be provided upon request.

Acknowledgments: We thank Boyan Zlatkov for leading the laboratory work, Maria Kachamakova and Yasen Mutafchiev for field assistance, and Stanimira Deleva, together with all the biologists conducting bat monitoring surveys in Bulgaria.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. O'Shea, T.J.; Ellison, L.E.; Stanley, T.R. *Survival estimation in bats: historical overview, critical appraisal and suggestions for new approaches.* In *Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters*; Thompson, W.L., Ed.; Island Press: Washington, DC, USA, **2004**; pp. 297–336.
2. Touzalin, F.; Petit, É.; Cam, E.; Stagier, C.; Teeling, E.C.; Puechmaille, S.J. *Mark loss can strongly bias estimates of demographic rates in multi-state models: a case study with simulated and empirical datasets. Peer Community Journal* 2023, *3*, e348. https://doi.org/10.24072/pcjournal.348
3. Blehert, D.S.; Hicks, A.C.; Behr, M.; Meteyer, C.U.; Berlowski-Zier, B.M.; Buckles, E.L.; et al. *Bat white-nose syndrome: an emerging fungal pathogen? Science* 2009, *323*(5911), 227. https://doi.org/10.1126/science.1163874

doi:10.20944/preprints202510.0852.v1

4. Fritze, M.; Puechmaille, S.J. *Identifying unusual mortality events in bats: a baseline for bat hibernation monitoring and white-nose syndrome research. Mammal Review* 2018, *48*(3), 224–228. https://doi.org/10.1111/mam.12122
5. O'Shea, T.J.; Cryan, P.M.; Hayman, D.T.S.; Plowright, R.K.; Streicker, D.G. *Multiple mortality events in bats: a global review. Mammal Review* 2016, *46*(3), 175–190. https://doi.org/10.1111/mam.12064
6. Vindenes, Y.; Langangen, Ø. *Individual heterogeneity in life histories and eco-evolutionary dynamics. Ecology Letters* 2015, *18*(5), 417–432. https://doi.org/10.1111/ele.12421
7. Lord, R.D.; Muradali, F.; Lázaro, L. *Age composition of vampire bats (Desmodus rotundus) in northern Argentina and southern Brazil. Journal of Mammalogy* 1976, *57*(3), 573–575. https://doi.org/10.2307/1379306
8. Schowalter, D.B.; Harder, L.D.; Treichel, B.H. *Age composition of some vespertilionid bats as determined by dental annuli. Canadian Journal of Zoology* 1978, *56*(2), 355–358. https://doi.org/10.1139/z78-049
9. Brunet-Rossinni, A.K.; Austad, S.N. *Ageing studies on bats: a review. Biogerontology* 2004, *5*(4), 211–222. https://doi.org/10.1023/b:bgen.0000038022.65024.d8
10. Toshkova, N.; Kolev, M.; Deleva, S.; Simeonov, T.; Popov, V. *Winter is (not) coming: Acoustic monitoring and temperature variation across important bat hibernacula. Biodiversity Data Journal* 2025, *13*, e141801. https://doi.org/10.3897/bdj.13.e141801
11. Dietz, C.; von Helversen, O. *Illustrated Identification Key to the Bats of Europe*; Vol. 1; Dietz & von Helversen: Tübingen, Germany, **2004**; pp. 1–74.
12. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, **2021**.
13. Batulevicius, D.; Paužienė, N.; Pauža, D.H. *Dental incremental lines in some small species of the European vespertilionid bats. Acta Theriologica* 2001, *46*(1), 33–42. https://doi.org/10.1007/bf03192414
14. Brunet-Rossini, A.K.; Wilkinson, G. *Methods for estimating age in bats.* In *Ecological and Behavioral Methods for the Study of Bats*, 2nd ed.; Kunz, T.H., Parsons, S., Eds.; The Johns Hopkins University Press: Baltimore, USA, **2009**; pp. 315–326.
15. Brunet-Rossinni, A.K.; Austad, S.N. *Ageing studies on bats: a review. Biogerontology* 2004, *5*(4), 211–222. https://doi.org/10.1023/b:bgen.0000038022.65024.d8
16. Ivanova, T. *Important bat underground habitats (IBuH) in Bulgaria. Acta Zoologica Bulgarica* 2005, *57*(2), 197–206.
17. Deleva, S.; Toshkova, N.; Kolev, M.; Tanalgo, K.C. *Important underground roosts for bats in Bulgaria: current state and priorities for conservation. Biodiversity Data Journal* 2023, *11*, e98734. https://doi.org/10.3897/bdj.11.e98734
18. Ivanova, T.; Petrov, B. *A new stage in bat (Chiroptera) research in Bulgaria. Historia naturalis bulgarica* 2001, *13*, 88. [In Bulgarian]
19. Fleischer, T.; Gampe, J.; Scheuerlein, A.; Kerth, G. *Rare catastrophic events drive population dynamics in a bat species with negligible senescence. Scientific Reports* 2017, *7*(1), 6298. https://doi.org/10.1038/s41598-017-06392-9
20. López-Roig, M.; Piera, E.; Serra-Cobo, J. *Thinner bats to face hibernation as response to climate warming. Scientific Reports* 2024, *14*(1), 1024. https://doi.org/10.1038/s41598-024-52459-9
21. Bernard, R.F.; Willcox, E.V.; Jackson, R.T.; Brown, V.A.; McCracken, G.F. *Feasting, not fasting: winter diets of cave hibernating bats in the United States. Frontiers in Zoology* 2021, *18*(1), 43. https://doi.org/10.1186/s12983-021-00434-9
22. Toshkova, N.; Dimitrova, K.; Langourov, M.; Zlatkov, B.; Bekchiev, R.; Ljubomirov, T.; et al. *Snacking during hibernation? Winter bat diet and prey availabilities, a case study from Iskar Gorge, Bulgaria. Historia naturalis bulgarica* 2023, *45*, 125–142. https://doi.org/10.48027/hnb.45.053
23. Constant, T.; Giroud, S.; Viblanc, V.A.; Tissier, M.L.; Bergeron, P.; Dobson, F.S.; et al. *Integrating mortality risk and the adaptiveness of hibernation. Frontiers in Physiology* 2020, *11*, 706. https://doi.org/10.3389/fphys.2020.00706
24. Theimer, T.C.; Dyer, A.C.; Keeley, B.W.; Gilbert, A.T.; Bergman, D.L. *Ecological potential for rabies virus transmission via scavenging of dead bats by mesocarnivores. Journal of Wildlife Diseases* 2017, *53*(2), 382–385. https://doi.org/10.7589/2016-09-203

25. Vicente, J.; VerCauteren, K.C. *The role of scavenging in disease dynamics.* In *Wildlife Research Monographs*; Springer: Cham, Switzerland, **2019;** pp. 161–182. https://doi.org/10.1007/978-3-030-16501-7_7
26. Mühldorfer, K.; Speck, S.; Wibbelt, G. *Diseases in free-ranging bats from Germany. BMC Veterinary Research* 2011, *7*(1), 61. https://doi.org/10.1186/1746-6148-7-61
27. Sriraman, P. *Wildlife Necropsy and Forensics*; CRC Press: Boca Raton, FL, USA, 2021. https://doi.org/10.1201/9781003172017
28. Colombino, E.; Lelli, D.; Canziani, S.; Quaranta, G.; Guidetti, C.; Leopardi, S.; et al. *Main causes of death of free-ranging bats in Turin province (north-western Italy): gross and histological findings and emergent virus surveillance. BMC Veterinary Research* 2023, *19*(1), 34. https://doi.org/10.1186/s12917-023-03776-0
29. Gol'din, P.; Godlevska, L.; Ghazali, M. *Age-related changes in the teeth of two bat species: dental wear, pulp cavity and dentine growth layers. Acta Chiropterologica* 2019, *20*(2), 519–526. https://doi.org/10.3161/15081109acc2018.20.2.022
30. Phillips, C.J.; Steinberg, B.M.; Kunz, T.H. *Dentin, cementum, and age determination in bats: a critical evaluation. Journal of Mammalogy* 1982, *63*(2), 197–207. https://doi.org/10.2307/1380628
31. Baagøe, H.J. *Age determination in bats (Chiroptera). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 1977, *140*, 53–92.
32. Cool, S.M.; Bennet, M.; Romaniuk, K. *Age estimation of pteropodid bats (Megachiroptera) from hard tissue parameters. Wildlife Research* 1994, *21*(3), 353–361. https://doi.org/10.1071/wr9940353
33. Wilkinson, G.S.; Adams, D.M.; Haghani, A.; Lu, A.T.; Zoller, J.A.; Breeze, C.E.; et al. *DNA methylation predicts age and provides insight into exceptional longevity of bats. Nature Communications* 2021, *12*(1), 1615. https://doi.org/10.1038/s41467-021-21900-2
34. Adams, D.M.; Rayner, J.G.; Hex, S.B.S.W.; Wilkinson, G.S. *DNA methylation dynamics reflect sex and status differences in mortality rates in a polygynous bat. Molecular Ecology* 2025, *34*(9), 2331–2346. https://doi.org/10.1111/mec.17745
35. Sendor, T.; Simon, M. *Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. Journal of Animal Ecology* 2003, *72*(2), 308–320. https://doi.org/10.1046/j.1365-2656.2003.00702.x