

# Elevational records of bats in Northwestern Italy

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## Abstract:

We report the elevational records (i.e. highest elevations) at which 29 bat species were recorded in Piedmont and Aosta Valley (NW Italy), an area that encompasses a sector of the Western Alps including some of the highest mountains in Europe.

Based on field data collected between 2018 and 2025, we identified new elevational records for 15 of the 29 species recorded in the area (*T. teniotis*, *B. barbastellus*, *E. nilssonii*, *E. serotinus*, *N. lasiopterus*, *N. leisleri*, *N. noctula*, *V. murinus*, *H. savii*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus*, *M. crypticus*, *M. daubentonii*, *M. mystacinus*). For the remaining species (*R. euryale*, *R. ferrumequinum*, *R. hipposideros*, *P. kuhlii*, *M. schreibersii*, *M. bechsteinii*, *M. blythii*, *M. brandtii*, *M. myotis*, *M. capaccinii*, *M. emarginatus*, *P. auritus*, *P. macrobullaris*, *P. austriacus*), elevational records were retrieved from both scientific and grey literature.

For each new elevational record, we provide date, geographic coordinates, a brief description of the site, and the criteria used for taxonomic identification. In addition, we list other noteworthy elevations where the 29 species were observed, including the highest known elevations for swarming and hibernation sites. We report for the first time the occurrence of *N. noctula* in Aosta Valley and confirm the presence of *N. lasiopterus*—previously recorded only once—in Piedmont.

With the exception of *M. schreibersii*, *R. euryale*, *M. capaccinii*, and *P. austriacus*, the elevational records listed are likely to be the highest recorded so far in Italy. To the best of our knowledge, those for *B. barbastellus*, *M. crypticus*, *M. daubentonii*, and *P. kuhlii* represent worldwide records.

**Keywords:** migration, climate change, altitude, Alps, Chiroptera, elevational records.

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## INTRODUCTION

At present, 1500 bat species are known worldwide, representing nearly a quarter of all described mammal species (Simmons and Cirranello 2025). Bats play essential roles in ecosystems and provide invaluable ecosystem services (Kunz et al. 2011). Because of their high sensitivity to several of the environmental stressors that characterize the Anthropocene (such as agricultural and industrial activities, forest management, energy production, urbanisation, hunting, and persecution), and their *K*-selected life history (populations can decline rapidly, while recovery rates tend to be slow), many bat species have experienced dramatic declines over the past century, leading to their inclusion in threatened species lists and the implementation of national and international protection measures (Racey and Entwistle 2003; Voigt and Kingston 2016). At the same time, bat susceptibility to environmental changes that affect many other taxa, together with their high taxonomic and ecological

33 diversity, wide geographic distribution, and relative ease of monitoring, make them excellent  
34 bioindicators, including for studies on climate change (Jones et al. 2009).

35 Changes in species ranges are among the most frequently investigated consequences of climate  
36 change on species (Lawlor et al. 2024), including bats (Festa et al. 2023). In Europe, range expansions  
37 toward higher latitudes, favoured by climate warming, have been observed in ecologically flexible  
38 species such as *Pipistrellus kuhlii* and *Hypsugo savii* (Sachanowicz et al. 2006; Uhrin et al. 2016;  
39 Ancillotto et al. 2016, 2018). In contrast, the possibility that other species—including *Myotis*  
40 *dasycneme*, *Eptesicus nilssonii*, *Nyctalus noctula*, and *Vespertilio murinus*—may face range  
41 contractions has been suggested based on distribution models (Rebelo et al. 2010). Changes in species  
42 distribution along the elevational gradient can be expected as well. Studies carried out in Central Italy  
43 documented a 175-meter upward shift over a 24 year period in the elevation reached by reproductive  
44 females of *Myotis daubentonii*, which was interpreted as a consequence of increased temperatures  
45 (Russo et al. 2024a; Belli et al. 2025).

46 Detecting and monitoring species distributional changes is challenging: it requires long-term  
47 investigations, runs up against the limits of identifiability of many species, and is complicated by the  
48 fact that range shifts may be driven by multiple factors beyond climatic ones, including habitat  
49 fragmentation, land use changes and other human modifications (Lawlor et al. 2024). At the same  
50 time, it may have important implications for conservation: it has been demonstrated that species  
51 interactions can play a critical role in determining range limits (e.g., Chan et al. 2019; Shepard et al.  
52 2021), and therefore it can be expected that species' range shifts—generating novel competition  
53 scenarios—may result in changes at the intraspecific (e.g., Belli et al. 2026) and interspecific level  
54 (e.g., Elmhagen et al. 2017).

55 To detect potential future shifts in bat distribution along elevational gradients, it is important to  
56 identify their current elevational distribution and upper elevation limits. European bats can occur at  
57 much higher elevations than previously believed, as revealed by surveys carried out in the Pyrenees  
58 (Alberdi et al. 2013, 2015), the Swiss Alps (Zingg et al. 2023), the Austrian Alps (Widerin and Reiter  
59 2017, 2018), and the Pirin Mountains in Bulgaria (Dundarova and Popov 2024). However, current  
60 knowledge on this topic is limited. Studies in high-elevation environments are complicated by  
61 weather conditions, which are often unfavorable for bat activity and thus for species detection; by the  
62 remoteness and risk associated to high-elevation survey sites which pose logistic constraints; or by  
63 environmental features which limit bat detectability (e.g., the high availability of water bodies—  
64 across which bats disperse to drink and forage—limits capture success, which is already low due to  
65 much lower bat population densities than in lowland and mid-elevation areas).

67 It has been emphasized that further studies are needed to avoid the risk of overlooking bats when  
68 assessing the impact of human activities at high elevations (e.g., Widerin and Reiter 2017; Caprio et  
69 al. 2020).

70 In this framework, our aim has been to report bat elevational records, meaning the highest elevation  
71 above the sea level at which each species has been observed, in the northwesternmost part of Italy,  
72 specifically within the administrative regions of Piedmont and Aosta Valley. This area includes a  
73 sector of the Western Alps that contains some of the highest peaks in Europe. Additionally, due to  
74 climatic differences (milder temperatures and higher humidity), mainly resulting from their closer  
75 proximity to the Atlantic Ocean, vegetation belts in the Western Alps extend to higher elevations than  
76 in the Central or Eastern Alps. These factors together suggest that many bat species are likely to reach  
77 their highest national elevation limits within this area, as observed for other vertebrates, such as *Rana*  
78 *temporaria* (Tiberti and Von Hardenberg 2012), *Coronella austriaca* and *Hierophis viridiflavus*  
79 (Tessa et al. 2017), and *Muscardinus avellanarius* (Bertolino et al. 2016).

80 Twenty-eight bat species are known to occur regularly in the study area (Patriarca et al. 2012;  
81 Patriarca and Debernardi 2021). A twenty-ninth species, *Nyctalus lasiopterus*, was recently recorded  
82 for the first time in the area (Vasenkov et al. 2023), yet, it remained unclear whether its occurrence  
83 resulted from a migratory or a dispersal event (Vasenkov et al. 2024; Russo et al. 2024b). For the  
84 total 29 species, representing 96.7% of the bat species regularly present in continental Italy (Loy et  
85 al. 2025), we assembled the elevational records and other notable high elevation data from recent bat  
86 surveys and a literature review. Since a substantial portion of the available evidence was fragmented  
87 and dispersed across difficult-to-access sources, the present work should be considered both an effort  
88 to explore high-mountain landscapes through dedicated monitoring and to synthesize and consolidate  
89 the existing information.

## 90 METHODS

### 91 Study area

92 The area of Piedmont and Aosta Valley (Fig. 1) is predominantly occupied by the western sector of  
93 Italian Alps (about 41% of the total surface), followed by the internal Piedmont hills (31%), the upper  
94 Po Valley (26%), and the northern sector of the Ligurian Apennines (2%).

95 Surveys covered a broad elevational gradient, ranging from lowland areas—mainly occupied by  
96 agroecosystems and urban settlements—and low hilly reliefs, primarily characterized by human-  
97 altered woodlands (dominated by *Robinia pseudoacacia* or *Castanea sativa* replacing *Quercus* spp.  
98 forests) and vineyards, to high-elevation alpine and subnival environments, across the multiple

100 vegetation and climatic belts of the Alps. Within this sector of the Alpine chain, several elevational  
101 vegetation belts can be distinguished: a basal belt (approximately below 800–900 m a.s.l.)  
102 characterized by deciduous broad-leaved forests originally dominated by *Quercus* spp., but strongly  
103 transformed by human land use (agroecosystems and spread of *Castanea sativa*); a montane belt  
104 (roughly 900–1400/1600 m a.s.l.) dominated by forests, mainly *Fagus sylvatica* and mixed  
105 conifer/broadleaf stands; a subalpine belt (approximately 1400/1600–2000/2300 m a.s.l.) marking the  
106 upper forest limit and gradually transitioning into more open woodlands (mainly dominated by *Larix*  
107 *decidua*, widely favoured by human activities), shrublands (frequently dominated by *Rhododendron*  
108 *ferrugineum* or *Alnus viridis*), and pastures; an alpine belt (about 2000/2300–2600/3000 m a.s.l.),  
109 where vegetation mainly consists of alpine grasslands, dwarf shrubs, and herbaceous communities  
110 adapted to harsh climatic conditions; and a nival belt (generally above 2600–3000 m a.s.l.)  
111 characterized by bare rocks, snowfields and ice. The elevational extent of these belts may vary slightly  
112 in relation to the relatively limited latitudinal gradient of the study area, but can vary substantially at  
113 the local scale due to microclimatic factors, including slope aspect, shading, exposure to wind and  
114 other atmospheric agents, and the presence of alpine lakes, which may increase primary and  
115 secondary production through water provision and lake-derived nutrients and prey subsidies.

### 116 **Field surveys**

117 We assembled the highest elevation data from several bat surveys conducted across different parts of  
118 the study area (Fig. 1) in the period 2018–2025. Although some surveys were conducted with different  
119 primary objectives, all of them contributed to improving knowledge of bat occurrence and  
120 distribution.

121 Classical bat surveying techniques were employed: acoustic recordings (to detect bats during their  
122 nighttime activity in different habitat-types or close to roost entrances), captures (carried out using  
123 mist-nets or harp-traps at foraging/drinking sites, along flight paths or at roost entrances), and  
124 inspections of potential roost sites (mainly caves, abandoned mines, and buildings).

125 The acoustic survey effort was important across the entire elevational range. By contrast, the survey  
126 effort using the other techniques was concentrated below 2,000 m, both because capture activities  
127 were more productive at these elevations (on average, 9.0 individuals per capture night below 2,000  
128 m compared to 2.8 individuals above 2,000 m), and due to the larger number and easier accessibility  
129 of potential roosts (Tab. 1).

130 Bats were identified according to Dietz and Kiefer (2016) and, when needed or useful to provide  
131 further evidence for the correct identification, based on acoustic recordings collected while releasing

133 them (used to discriminate *P. pipistrellus* and *P. pygmaeus*) or molecular analyses of wing biopsies  
134 or faeces (for *Plecotus* spp.; methodological details in S1).

135 Acoustic surveys were generally repeated during summer and early autumn in order to sample both  
136 resident and migrating bats. For most recording points, sampling was carried out systematically over  
137 multiple nights per month, and in some cases repeated over more years. We employed passive bat  
138 detectors (SM2BAT+, SM4BAT FS, and Song Meter Mini Bat Ultrasonic Recorder, Wildlife  
139 Acoustics Inc.; AudioMoth 1.2.0., Silicon Labs), operated with a sampling frequency of 384 kHz.  
140 When in high numbers, the recordings were first analysed using the automatic classifier Tadarida  
141 (Bas et al. 2017) in order to obtain a preliminary association of the calls to bat species and exclude  
142 the files attributed by the software to other sources (insects, birds, small mammals, noise). Each bat  
143 species occurrence was then manually validated. Calls were measured as described by Barataud  
144 (2020), using BatSound 4.03 (Pettersson Elektronik AB, Uppsala, Sweden), Kaleidoscope Lite (5.4.9  
145 and 5.6.8, Wildlife Acoustics, Maynard, USA) or BatExplorer (2.1 and 2.2, Elekon AG, Lucerna,  
146 Switzerland). Identification criteria of echolocation and social calls were derived from several  
147 literature sources, primarily Barataud (2020), Russ (2021), and Middleton et al. (2022). Since  
148 literature sources do not always agree on the identification criteria, we specify the exact criteria that  
149 we adopted on a case-by-case basis in the presentation of the results. To ensure accurate species  
150 identification, we applied highly conservative criteria, and in cases of even moderate uncertainty, we  
151 opted for cautious assignments—such as higher taxonomic levels (e.g., *Myotis* sp.) and groups of  
152 species with similar calls (e.g., *P. kuhlii*/*P. nathusii*)—or we discarded the calls. We made exceptions  
153 in a few cases where the available evidence allowed the identification as “probable”, for example,  
154 when social calls resembling those described in the literature for a given species were present, but  
155 knowledge of the calls of potentially confusable species remains lacking. Moreover, for each new  
156 elevational record we provide a spectrogram showing a representative portion of the acoustic  
157 sequence recorded.

### 158 **Literature review and data extraction**

159 In a preliminary phase of the research, we followed the standard PRISMA (Preferred Reporting Items  
160 for Systematic Reviews and Meta-Analyses) procedure to identify documents and peer-reviewed  
161 articles published in the Scopus and Web of Science databases that were relevant to the topic of the  
162 present study, covering publications up to 9 March 2026 (Page et al. 2021). The search strategy was  
163 structured using Boolean operators and truncation symbols and was applied to titles, abstracts, and  
164 keywords (TITLE-ABS-KEY in Scopus; Topic search in Web of Science). Specifically, the following  
165 search string was used: (" bat\*" OR "chiroptera\*") AND (((("elevation\*" OR "altitud\*") AND

167 ("limit\*" OR "gradient\* ") OR ("high" AND ("altitud\*" OR "elevation\*")) AND ("Italy" OR  
168 "Europe" OR "Alps") NOT ("bath\*" OR "batt\*" OR "batr\*" OR "batch\*"). We anticipate that this  
169 process yielded 43 papers from Scopus and 33 from Web of Science, which formed the basis for a  
170 subsequent in-depth examination of the full texts and their bibliographies. After screening the content  
171 of the retrieved papers, only 18 provided information relevant to the aims of this study (i.e.,  
172 elevational distribution of bats) and only eight studies specifically addressed the assessment of  
173 elevational limits. Overall, the final set of studies obtained through this procedure provided a very  
174 limited contribution to the literature of interest, both in quantitative terms and in terms of effective  
175 coverage of the available evidence. In the context of this study, standard PRISMA procedures proved  
176 insufficient to capture the full breadth of existing information about bat elevational limits, as a  
177 substantial portion of relevant evidence is fragmented and dispersed across local datasets, region-  
178 specific technical reports, institutional documentation, and other forms of grey or non-indexed  
179 literature that are not systematically retrieved through conventional bibliographic search strategies.  
180 This result supported our methodological decision to broaden the literature search by adopting an  
181 expert-based approach grounded in the authors' knowledge of local and regional sources.  
182 Accordingly, the present work should be considered a synthesis effort aimed at consolidating  
183 heterogeneous and fragmented information into a coherent and comprehensive evidence base, thereby  
184 providing a more representative overview of the current state of knowledge.

185 Following this search strategy, the core set of information obtained through the standard PRISMA  
186 procedure was thus complemented by additional searches in published scientific literature and, in  
187 particular, in grey literature. The search was facilitated by the access of an almost complete library  
188 of historical and recent chiropterological works from the study area, including old speleological  
189 reports and unpublished documents on monitoring activities and environmental assessments, as well  
190 as by existing databases and studies that had already aggregated previous historical, museum, and  
191 speleological bulletin data (in particular: Gulino 1938; Sindaco et al. 1992; Agnelli 2006; Lanza 2012;  
192 Lana et al. 2021; Patriarca and Debernardi 2021, and the cave database of Piedmont and Aosta  
193 Valley). A distinctive aspect of this research is that some of the retrieved data were corrected,  
194 commented, or supplemented, ensuring both accuracy and comprehensiveness. Since some old data  
195 have been repeatedly cited in successive papers, often resulting in an accumulation of mistakes (for  
196 example concerning the date or the nature of the observations), we focused on the original sources  
197 and validated each datum according to the current systematic knowledge and identification criteria.  
198 In some cases, we cited literature sources as "supplemented", indicating that we have included  
199 additional information not present in the original sources, but provided by their authors.

201 Regarding data collected in caves, we often noticed differences between the elevation of the cave  
202 entrances reported in literature and those recorded in the cave database of Piedmont and Aosta Valley.  
203 The latter is likely more correct; nevertheless, in such cases we reported both values, in order to  
204 ensure traceability to former literature sources.

### 205 **Reporting of elevational data**

206 For each new elevational record, we provide data including date of the observation, geographic  
207 position (specifying in this order: coordinates, closest toponym, municipality and province), a brief  
208 environmental description, and the criteria applied for taxonomic identification. In the case of  
209 acoustic identification, we report the characteristics of the calls and the values of the acoustic  
210 parameters considered to be more discriminant, to which we refer using the following abbreviations:  
211 CF= constant frequency, QCF= quasi-constant frequency, FM= frequency modulated, FmaxE=  
212 frequency of the maximum amplitude of the spectrum, SF= frequency at the start of the call, EF=  
213 frequency at the end of the call, BL= bandwidth length of the call, dur= duration of the call, IPI=  
214 interval between the start of two consecutive calls. We consider QCF calls those with a BL < 5kHz.  
215 Together with elevational records, we list other data regarding notable elevations at which the species  
216 were recorded, including:

- 217 - all the occurrences recorded at sites located higher than the previous elevation record;
- 218 - if relevant to shed light on some aspects characterizing species occurrence (such as seasonality and  
219 local abundance), further data recorded at sites located below the elevation record;
- 220 - notable elevations where feeding buzzes were recorded or individuals were captured;
- 221 - highest elevations of the known autumn swarming sites, classified as such based on bat behaviour  
222 (flying in and out of caves and mines at night) and the capture of numerous individuals—mainly  
223 males from multiple species—primarily occurring between mid-August and the end of September;
- 224 - highest elevations of the known hibernation sites, classified as such based on the observation of  
225 hibernating bats from the beginning of December to the end of February.

226 For all these data we report the location; in addition, we report the precise date for captures and  
227 observations inside roosts, and the month and year for acoustic recordings. For ease of reading we  
228 omit the day in the case of the latter, since acoustic surveys were often conducted over multiple  
229 consecutive nights within the same month, leading to repeated recordings.

230 Elevations of lakes and underground sites were obtained from the corresponding regional databases  
231 (<https://mappe.regione.vda.it/pub/GeoNavSCT/index.html?metadato=MTD210N0001>;  
232 <https://catastogrotte-piemonte.net/>). In all other cases, we located the recording sites by using GPS  
233 devices (Garmin GPSMAP 65s and Garmin Oregon 300) and gave the corresponding elevation

235 according to regional technical maps (<https://geoportale.regione.vda.it/download/ctr/>;  
236 <https://geoportale.igr.piemonte.it/cms/>).

## 237 RESULTS

238 In the following section, we present species-by-species accounts; readers primarily interested in an  
239 overall summary can refer to the “Overall results” section at the end of the Results.

### 240 Elevation data for each species

#### 241 Family Miniopteridae

##### 242 *Miniopterus schreibersii*

243 The Schreiber’s bent-winged bat is uncommon in the study area: its occurrence in Aosta Valley,  
244 although possible, has never been ascertained (Patriarca and Debernardi 2021), and in Piedmont the  
245 data obtained through capture or by direct visual observation regard few individuals observed at a  
246 small number of sites (Toffoli 2025; Debernardi et al. 2025).

247 The elevational record was collected in the Apennines, at 1,550 m (Alta Val Curone, Fabbrica Curone,  
248 Alessandria), where Toffoli (2025) recorded echolocation calls considered diagnostic for  
249 identification (FMQCF calls with final FmaxE >50 kHz, and dur >10 ms) on 26 April 2022 and 3  
250 September 2022.

251 From 2018 to 2025, 1–4 hibernating individuals have been repeatedly observed and photographed in  
252 a cave at 1,530 m (44.69907, 7.14612, Grotta di Rio Martino, Crissolo, Cuneo) (Patriarca et al. 2019;  
253 Toffoli 2019). A female was captured while exiting from the same site on 15 March 2019 (Garzoli et  
254 al. 2021).

255 Sindaco et al. (1992) reported the collection of a museum specimen in the cave Grotta dei Partigiani  
256 on 28 June 1986. The authors situate the cave, without specifying its elevation, in the locality of  
257 Artesina and the municipality of Frabosa Soprana. In fact, Artesina is in the municipality of Frabosa  
258 Sottana, and the Grotta dei Partigiani, according to the speleological database, is situated at 1,760 m  
259 in a different, although close, municipality (44.24087, 7.73324, Grotta dei Partigiani, Roccaforte  
260 Mondovì, Cuneo). Toffoli (2025) has recently cited the same finding as referring to a “sub-fossil  
261 skull”, thus of possible ancient origin. Unfortunately, the museum collection in which the specimen  
262 was preserved is no longer extant (D. Scaravelli, pers. comm.), so we have not been able to collect  
263 further information on this finding.

265 However, the occurrence of this species higher than ascertained is probable. We have recorded  
266 echolocation calls of uncertain specific attribution within the group *P. pipistrellus*/*M. schreibersii*/*P.*  
267 *pygmaeus* up to 2,703 m (45.49367, 7.13216, Lago Leità, Ceresole Reale, Torino; August 2024).

#### 268 Family Molossidae

##### 269 *Tadarida teniotis*

270 The previous maximum elevation recorded for this species (2,560 m) was reported for the Gran  
271 Paradiso National Park (Patriarca et al. 2018). In the same area, on 25 September 2023 we recorded  
272 sequences of echolocation calls emitted by European free-tailed bats (e.g., Fig. 2A: FM calls, FmaxE  
273 17.4–18.1kHz, EF 13–13.9 kHz, dur 11.8 ms, IPI 811 ms) at 3,046 m (45.48861, 7.25431, Colle della  
274 Torre, Noasca, Torino). Moreover, we frequently recorded sequences of QCF calls (FmaxE  $\leq$  12 kHz,  
275 duration mainly  $<17$  ms and IPI mainly  $<600$  ms) at the following elevations above the former  
276 elevational record: 2,749 m (45.51409, 7.16105, near Pian Borgnoz, Valsavarenche, Aosta; August  
277 2024), 2,747 m (45.50773, 7.15189, Lago Leynir, Valsavarenche, Aosta; September 2023, July  
278 2024), 2,737 m (45.50212, 7.14768, Laghi Trebecchi, Valsavarenche, Aosta; July and August 2024),  
279 2,703 m (45.49367, 7.13216, Lago Leità, Ceresole Reale, Torino; September 2022, August 2024),  
280 and 2,568 m (45.47573, 7.15701, Lago Losere, Ceresole Reale, Torino; August 2025). We recorded  
281 feeding buzzes up to 2,703 m (45.49367, 7.13216, Lago Leità, Ceresole Reale, Torino; August 2024).  
282 Outside the Gran Paradiso National Park, we gathered further evidence of the usual summer  
283 occurrence of this species at high elevations, for example at 2,564 m (45.63962, 7.54858, Lago Gran  
284 Betassa IX, Champdepraz, Aosta; September 2022, August 2023, July and August 2024), 2,484 m  
285 (45.04795, 6.93273, near Colle Lauson, Salbertrand, Torino; July, August, September, and October  
286 2022), and 2,435 m (45.07136, 6.95578, near Colle dell'Assietta, Exilles, Torino; July, August,  
287 September, and October 2022).

288 All the above-listed sites are characterized by mosaics of rock debris, alpine prairie, glacial lakes and  
289 rock walls.

290 Current knowledge about wintering sites is scarce and limited to areas of low elevation.

#### 291 Family Rhinolophidae

##### 292 *Rhinolophus euryale*

293 Occurrences of this species are currently known only for two caves in the southern part of the study  
294 area. In one of them, situated at 1,030 m (44.17429, 7.96839, Arma Inferiore dei Grai, Ormea, Cuneo),  
295 observations of individuals were reported following surveys carried out in autumn 2009 and winter  
296 2011/12 (Patriarca et al. 2012 supplemented). In the other cave, at 920 m (44.16195, 7.94746, Grotta

298 della Pecora, Ormea, Cuneo), hibernating individuals were observed on 10 February 2018 (Lana et  
299 al. 2019).

300 Older data (Dinale 1967) are limited to two observations, which were recorded at lower elevations  
301 and cannot, at any rate, be considered of current relevance.

### 302 *Rhinolophus ferrumequinum*

303 We recorded sequences of echolocation calls emitted by greater horseshoe bats (FM-CF-FM calls  
304 with FmaxE peaking at 79–81 kHz) at 1,801 m (44.77311, 7.04630, near Conca del Prà, Bobbio  
305 Pellice, Torino) on 29 July 2024 (Fig. 2B), and at 1,712 m (45.66903, 7.49375, Val Clavalitè, Fenis,  
306 Aosta) on 6 September 2021. Both recordings were collected in coniferous woods dominated by larch,  
307 with rich shrubby understorey and presence of large boulders.

308 The highest roost sites known are two caves situated at 1,947 m (44.15792, 7.71098, Arma delle  
309 Mastrelle, Briga Alta, Cuneo) and 1,590 m (44.12933, 7.93332, Garb del Dighea, Ormea, Cuneo),  
310 where single torpid individuals were observed respectively on 10 March 1998 (Pascutto and  
311 Balestrieri 2000) and 17 October 2019 (Lana et al. 2021). Hibernating individuals are regularly  
312 observed in a cave at 1,558 m (44.15148, 7.75133, Grotta delle Vene, Ormea, Cuneo) (Lana et al.  
313 2021).

314 The record reported by Bologna and Vigna Taglianti (1985) for a cave localised at 2,180 m, which  
315 the speleological database places at 2,155 m (44.14723, 7.70798, Carsena del Ferà, Briga Alta,  
316 Cuneo), cannot be considered reliable because it was based on the finding of undated remains, which  
317 occurred on 12 August 1967. Afterwards, Sindaco et al. (1992) wrongly reported that it derived from  
318 the direct observation of living bats.

### 319 *Rhinolophus hipposideros*

320 One torpid individual was observed in a cave at 1,760 m (44.15273, 7.76460, Carsena di Viora,  
321 Ormea, Cuneo) on 4 November 2019 (Lana et al. 2021). The site currently known to host the largest  
322 number of hibernating individuals is a cave at 1,558 m (44.15148, 7.75133, Grotta delle Vene, Ormea,  
323 Cuneo) (Lana et al. 2021).

324 We recorded sequences of echolocation calls emitted by lesser horseshoe bats (FM-CF-FM calls with  
325 FmaxE peaking at 107–114 kHz) at 1,692 m (44.48722, 6.98778, near Grano Ciabota, Acceglio,  
326 Cuneo; June 2025), 1,640 m (44.50194, 6.91750, near Forte dei Mulattieri, Acceglio, Cuneo; June  
327 2025), and 1,551 m (44.47917, 6.93167, near Pianore Duella, Acceglio, Cuneo; June 2025).

328 Two older literature data were collected at higher elevations: between 1991 and 2002, in  
329 August/September, single individuals were observed in two caves, which were identified as Abisso

331 Ngoro-Ngoro and Buco delle Maestrelle (Toffoli 2005). The first cave was reported at 2,000 m, citing  
332 the toponym of Prato Nevoso (a locality in the municipality of Frabosa Sottana, Cuneo), but the  
333 speleological database locates the cave named Abisso Ngoro-Ngoro at 2,182 m, in the municipality  
334 of Roccaforte Mondovì (Cuneo), thus making the actual elevation of the observation unclear. The  
335 cave Buco delle Maestrelle (syn. Arma delle Maestrelle, 44.15792, 7.71098, Briga Alta, Cuneo) was  
336 correctly located, although with a slight discrepancy between the elevation of the cave entrance  
337 reported in the paper (1,927 m) and in the speleological database (1,947 m). Taken together, these  
338 older data can be summarized as relating to an elevation of approximately 2,000 m.

### 339 Family Vespertilionidae

#### 340 *Barbastella barbastellus*

341 The previous maximum elevation of 2,292 m corresponded to a site (45.46018, 7.13382, near Lago  
342 Serrù, Ceresole Reale, Torino) where a male western barbastelle was captured on 12 August 2015  
343 (Patriarca et al. 2018 supplemented). At a slightly lower elevation—2,208 m (45.86133, 7.15964;  
344 Casa Carioni, Saint-Rhémy-En-Bosses, Aosta)—the species was recorded through acoustic surveys  
345 (Caprio et al. 2020) in September 2016; this observation was later incorrectly cited by Toffoli and  
346 Cucco (2020) as occurred at an elevation of 2,470 m.

347 On 29 and 30 August 2024 we recorded three sequences of echolocation calls due to this species (e.g.,  
348 Fig. 2C: FM calls, FmaxE 32.7 kHz, SF 36.1 kHz, EF 28.6 kHz, dur 2.7 ms, IPI 115.2 ms) at 2,703  
349 m (45.49367, 7.13216, Lago Leità, Ceresole Reale, Torino). Moreover, we detected its occurrence  
350 from echolocation calls (sequences characterised by alternation between loud short-banded FM calls  
351 with FmaxE around 31–34 kHz and QCF-FM calls peaking at 38–43 kHz, or composed of only one  
352 of these two call types) at the following other elevations above the maximum previously recorded:  
353 2,534 m (45.48238, 7.14497, Lago Nivolet Superiore, Valsavarenche, Aosta; September 2022), 2,526  
354 m (45.48622, 7.14619, Lago Nivolet Inferiore, Valsavarenche, Aosta; September 2022), 2,484 m  
355 (45.04795, 6.93273, near Colle Lauson, Salbertrand, Torino; August and September 2022), 2,443 m  
356 (45.46671, 7.15237, Casotto PNGP di Bastalon, Ceresole Reale, Torino; August 2024), 2,435 m  
357 (45.07136, 6.95578, near Colle dell'Assietta, Exilles, Torino; August 2022), 2,412 m (44.98746,  
358 6.86787, near Colle Basset, Sestriere, Torino; September and October 2022), 2,403 m (45.47075,  
359 7.25615, Alpe di Breuil, Noasca, Torino; August 2025), 2,347 m (45.03791, 6.91427, near Colle  
360 Blegier, Oulx, Torino; October 2022), and 2,320 m (45.02270, 6.89885, near Colle Costapiana, Sauze  
361 d'Oulx, Torino; August 2022).

362 In late August and September individuals have been observed at various underground sites, the  
363 highest of which is a cave at 1,930 m (44.18862, 7.90124, Rem del Ghiaccio, Garessio, Cuneo) where  
364

365 the occurrence of the species was discovered in 2016 (Lana and Balestra 2018). The hibernation sites  
366 of highest elevation currently known are an abandoned mine at 1,903 m (45.67931, 7.44917,  
367 Praborna, Saint-Marcel, Aosta), whose use by the species was documented from 2021 to 2025  
368 (Patriarca and Debernardi 2021 supplemented), and a fortification at 1,880 m (45.049487, 7.048512,  
369 Forte Serre Marie, Fenestrelle, Torino), which we surveyed on 11 February 2024.

### 370 *Eptesicus nilssonii*

371 The northern bat is rare in the study area, although some isolated data prove that its distribution  
372 extends southward to the Maritime Alps (Toffoli et al. 2016).

373 The elevational record reported in previous literature derives from acoustic contacts recorded at 2,460  
374 m (45.49624, 7.15819, Piano del Nivolet, Valsavarenche, Aosta) in the Gran Paradiso National Park  
375 (Patriarca et al. 2018). In the same area, on 28 July 2024, we recorded some echolocation calls of this  
376 species (e.g., Fig. 2D: QCF calls, FmaxE 28 kHz, SF 29.4 kHz, EF 27.8 kHz, dur 15 ms) at 2,703 m  
377 (45.49367, 7.13216, Lago Leità, Ceresole Reale, Torino), on the shore of a glacial lake surrounded  
378 by rock debris and, to a lesser extent, alpine prairie.

379 We recorded further acoustic contacts (QCF calls with FmaxE 28–29.5 kHz, EF 27–29 kHz, dur 11–  
380 20 ms) at 2,526 m (45.48622, 7.14619, Lago Nivolet Inferiore, Valsavarenche, Aosta; July and  
381 August 2024, July and August 2025), 2,475 m (45.44305, 7.13432, Alpe Rocce Piccole, Ceresole  
382 Reale, Torino; July 2024), 2,472 m (45.47211, 7.15001, Laghi della Civetta, Ceresole Reale, Torino;  
383 August 2024), and 2,396 m (45.42761, 7.18159, Lago di Nel, Ceresole Reale, Torino; July and August  
384 2024). We observed feeding buzzes up to 2,475 m (45.44305, 7.13432, Alpe Rocce Piccole, Ceresole  
385 Reale, Torino; July 2024).

386 A male northern bat was captured at 1,800 m (Lourousa Valley, Valdieri, Cuneo; 12 July 2012)  
387 (Toffoli et al. 2016).

388 There is no information about roosts used by this species to hibernate or for other biological functions.

### 389 *Eptesicus serotinus*

390 The elevational record previously published was obtained through acoustic recording at 2,156 m  
391 (45.61848, 7.54952, near Dondenaz, Champorcher, Aosta) on 17 July 2021 (Patriarca and Debernardi  
392 2021 supplemented). This elevation was exceeded by that of a site at 2,275 m (44.88304, 7.12177,  
393 Conca Cialancia Natural Park, Perrero, Torino) characterised by a mosaic of rocks, herbs and  
394 prostrate shrubs, with presence of some isolated small larches. There, from 17 to 21 July 2018, we  
395 recorded several echolocation sequences (e.g., Fig. 2E: FM-QCF calls, FmaxE 27.3 kHz, SF 60.8

397 kHz, EF 23.5 kHz, dur 12 ms), some of which were followed by social calls with the characteristics  
398 referred by Pflazer (2002) to the “B type” of this species (Fig. 2F).

399 We recorded further analogous sequences of echolocation calls at 1,965 m (45.82241, 7.61953, Col  
400 Pilaz, La Magdeleine, Aosta; August 2020), 1,960 m (45.71279, 7.59481, Grotta Alta di Valmeriana,  
401 Pontey, Aosta; June 2021), and 1,780 m (45.45691, 7.17158, Chiapili di Sopra, Ceresole Reale,  
402 Torino; July 2013).

403 A male serotine was captured at 1,618 m (45.59505, 7.38682, Lillaz, Cogne, Aosta; 1 September  
404 2013) (Patriarca et al. 2018 supplemented).

405 Some hibernating individuals are irregularly observed in caves at 1,558 (44.15148, 7.75133, Grotta  
406 delle Vene, Ormea, Cuneo; 14 February 2009) (Lana et al. 2021 supplemented) and 1,530 m  
407 (44.69907, 7.14612, Grotta di Rio Martino, Crissolo, Cuneo; winter 2016/2017) (Toffoli 2019).

#### 408 *Hypsugo savii*

409 The previous highest elevation was obtained through acoustic recording at 2,460 m (45.49624,  
410 7.15819, Piano del Nivolet, Valsavarenche, Aosta), in the Gran Paradiso National Park (Patriarca et  
411 al. 2018). In an area of rocky debris of the same Park, on 9 and 10 August 2024, we recorded eight  
412 echolocation sequences emitted by this species (e.g., Fig. 2G: QCF calls, FmaxE 32.7 kHz, SF 33.4  
413 kHz, EF 31.0 kHz, dur 12.7 ms) at 2,853 m (45.47245, 7.19421, near Lago Gias di Beu, Ceresole  
414 Reale, Torino).

415 Moreover, we recorded many other echolocation calls attributable to the Savi’s pipistrelle (QCF calls  
416 with FmaxE 30.5–33.5 kHz or FM-QCF calls with FmaxE 33–34 kHz, EF 31–33 kHz and BL  $\leq$ 13  
417 kHz) at the following other elevations above the previous maximum: 2,850 m (45.49859, 7.33700,  
418 Colle dei Becchi, Locana, Torino; August 2023), 2,827 m (45.46655, 7.21506, near Lago Lillet,  
419 Ceresole Reale, Torino; August 2025), 2,773 m (45.46682, 7.20968, Lago Lillet, Ceresole Reale,  
420 Torino; August and September 2025), 2,737 m (45.50212, 7.14768, Laghi Trebecchi, Valsavarenche,  
421 Aosta; August 2024), 2,703 m (45.49367, 7.13216, Lago Leità, Ceresole Reale, Torino; August  
422 2023), 2,568 m (45.47573, 7.15701, Lago Losere, Ceresole Reale, Torino; July 2024, August 2025),  
423 2,564 m (45.63962, 7.54858, Lago Gran Betassa IX, Champdepraz, Aosta; August 2023, July and  
424 August 2024, July and August 2025), 2,526 m (45.48622, 7.14619, Lago Nivolet Inferiore,  
425 Valsavarenche, Aosta; September 2022, August 2023, July and August 2024, July and August 2025),  
426 2,520 m (45.63962, 7.54858, Lago Gran Betassa I, Champdepraz, Aosta; September 2022, August  
427 2023, July and August 2024, July and August 2025), 2,484 m (45.04795, 6.93273, near Colle Lauson,  
428 Salbertrand, Torino; July, August, September, and October 2022), and 2,482 m (45.47760, 7.27510,

430 Lago inferiore di Ciamousseretto, Noasca, Torino; June and August 2023). We recorded feeding  
431 buzzes up to 2,827 m (45.46655, 7.21506, near Lago Lillet, Ceresole Reale, Torino; August 2025).  
432 We mistnetted some individuals at 2,402 m (45.59670, 7.46001, Alpe Broillot, Cogne, Aosta; one  
433 male; 9 July 2020) and 2,291 m (44.77461, 7.06096, Giardino Alpino Peyronel, Bobbio Pellice,  
434 Torino; one female and 11 males; 3 August 2024).  
435 A hibernating individual has been observed in a cave at 1,558 m (44.15148, 7.75133, Grotta delle  
436 Vene, Ormea, Cuneo) on 26 January 2006 (Lana et al. 2021 supplemented).

#### 437 *Myotis bechsteinii*

438 In 2018, IR photographs of individuals of this species were taken in a cave at 1,530 m (44.69907,  
439 7.14612, Grotta di Rio Martino, Crissolo, Cuneo) during autumn swarming (Patriarca et al. 2019). A  
440 male had already been captured at the entrance of the same site in September 2009 (Toffoli 2019) and  
441 other two males were captured while exiting from the cave on 10 June 2018 (Patriarca et al. 2019).  
442 Bechstein's bat probably uses the cave to hibernate as well, but no winter observations of individuals  
443 are known either for this or for other sites in the study area.

444 Considering its elusiveness, we expect it may occur at higher elevations. Nevertheless, the record  
445 reported by Amelio and Bonzano (1986) at 2,435 m (referred to the cave Abisso dei Caproschi,  
446 Magliano Alpi, Cuneo, whose exact elevation, according to the regional speleological database, is  
447 2,419 m), cannot be considered of current value since it was based on the finding (in the 1970s or  
448 early 1980s) of an undated skull, which might have been ancient.

#### 449 *Myotis blythii*

450 Recent highest data are due to captures at swarming sites: a cave at 1,930 m (44.18862, 7.90124, Rem  
451 del Ghiaccio, Garessio, Cuneo), where one individual was captured in September 2016 (Lana and  
452 Balestra 2018 supplemented), a mine gallery at 1,670 m (45.69673, 7.63538, mines of Hérin,  
453 Champdepraz, Aosta) where two females were captured on 17–18 August 2021 (Patriarca and  
454 Debernardi 2021 supplemented), and a cave at 1,530 m (44.69907, 7.14612, Grotta di Rio Martino,  
455 Crissolo, Cuneo), where 1–3 individuals of *M. blythii* were captured in September 2009 and 2010  
456 (Toffoli 2019). The latter site is regularly used by this species also to hibernate (Patriarca et al. 2019;  
457 Toffoli 2019) and, as a resting site, in spring and summer (Patriarca et al. 2019; Garzoli et al. 2021).  
458 To date, the highest record refers to a male which was mistnetted while flying over alpine pastures at  
459 2,000 m (44.14955, 7.56188, Colle di Tenda, Limone Piemonte, Cuneo) (Sindaco et al. 1992); yet,  
460 the date of the capture—19 August 1987—does not allow to consider it of current value.

462 *Myotis myotis*

463 The highest record of this species was obtained at a swarming site: an individual was captured in  
464 September 2010 at the entrance of a cave at 1,530 m (44.69907, 7.14612, Grotta di Rio Martino,  
465 Crissolo, Cuneo) (Toffoli 2019). Six other individuals—all males—were mistnetted at the entrance of  
466 an artificial gallery located at about 1,500 m in the municipality of Limone Piemonte; the date of the  
467 capture was not specified (Toffoli et al. 2016).

468 *M. blythii/M. myotis*

469 Some echolocation sequences recorded in June 2015 over a mosaic of peat bogs and alpine prairie at  
470 2,460 m (45.49624, 7.15819, Piano del Nivolet, Valsavarenche, Aosta) were attributed to the *M.*  
471 *blythii/M. myotis* pair by Patriarca et al. (2018). The authors later reconsidered the record as doubtful  
472 due to both the high elevation of the recording site and the considerable distance from the nearest site  
473 where the presence of mouse-eared bats was visually ascertained (Patriarca and Debernardi 2021).  
474 Nevertheless, the characteristics of the calls (FM with warbling shape, FmaxE 31.3 kHz, SF 73.3  
475 kHz, EF 23.6 kHz, dur 8.7 ms) and the recent recording of analogous echolocation calls at other sites  
476 above 2,000 m led us to confirm their attribution to mouse-eared bats. We recorded the calls at 2,291  
477 m (44.77461, 7.06096, Giardino Alpino Peyronel, Bobbio Pellice, Torino; August 2024), 2,209 m  
478 (44.78154, 7.05592, near Colletta, Bobbio Pellice, Torino; July 2024), 2,177 m (45.68084, 6.88600,  
479 near Colle del Piccolo San Bernardo, La Thuile, Aosta; August 2022), and 2,035 m (45.075658,  
480 7.053834, below Colle delle Finestre, Meana di Susa, Torino; July 2022).

481 A torpid mouse-eared bat was photographed on 23 October 2010 in a mine gallery at 1,870 m  
482 (44.84478, 7.10251, mines of Subiasco, Villar Pellice, Torino) (Jannin and Magri 2015). We observed  
483 single hibernating individuals inside mine galleries at 1,670 m (45.69673, 7.63538, mines of Hérin,  
484 Champdepraz, Aosta) on 4 January 2021 and at 1,640 m (45.75350, 7.74566, Chamousira mine,  
485 Brusson, Aosta) on 10 February 2020.

486 An observation carried out in the 1970s in a cave located at 2,230 m (Grotta C-25 di Monte Rotondo,  
487 Ormea, Cuneo; not included in the speleological database) was referred to mouse-eared bats by  
488 Sindaco et al. (1992), who cited Calandri (1976) and Bologna and Vigna Taglianti (1985). However,  
489 the original literature source (Calandri 1976) referred to a *Myotis (Selysius)* sp. and Bologna and  
490 Vigna Taglianti (1985) mentioned it as a *Myotis* sp.

491 *Myotis brandtii*

492 Within the study area, this species is known to occur only in the northern part of Piedmont, where it  
493 has been captured for the first time in August 2005 on a peat bog surrounded by larch wood at 1,827

495 m (near Alpe Devero, Baceno, Verbano-Cusio-Ossola) (Toffoli 2006). Afterwards, during the  
496 summer of 2010, some individuals were captured at about 1,640 m in the same area (Piana di Devero,  
497 Baceno, Verbano-Cusio-Ossola) and at 1,720 m in a nearby valley (Piana di Veglia, Varzo, Verbano-  
498 Cusio-Ossola) (Toffoli and Culasso 2015).

499 There are no data about hibernacula.

### 500 *Myotis capaccinii*

501 This species is currently known to occur in the study area only at one site, located at 205 m, on one  
502 of the small islands of Lake Maggiore (45.89464, 8.52840, Isola Bella, Stresa, Verbano-Cusio-  
503 Ossola). On the island it uses an artificial underground to breed, probably to mate and, limited to a  
504 few individuals, also to hibernate (Debernardi and Patriarca 2007; Debernardi et al. 2012; Garzoli et  
505 al. 2025). The main hibernacula of the long-fingered bats observed at the site are believed to be in the  
506 adjacent region of Lombardy, where some caves and mines are known to be used by this species  
507 during winter (Debernardi et al. 2012; Spada et al. 2018).

508 The other few data available for the study area date back to the first half of the twentieth century or  
509 to the nineteenth century, and are all referred to elevations below 300 (Gulino 1938; Sindaco et al.  
510 1992).

### 511 *Myotis crypticus*

512 Currently this is the only species of the *Myotis nattereri* complex ascertained to occur in NW Italy  
513 (Galimberti et al. 2012; Salicini et al. 2013); unless this assumption is disproved by further  
514 knowledge, the data once attributed to *M. nattereri* should be also referred to it.

515 The former elevational record was obtained through acoustic recordings collected at 2,323 m on 18  
516 July 2020 (Saint-Marcel, Aosta) (Patriarca and Debernardi 2021).

517 On 29 August 2022 we recorded echolocation and social calls (Fig. 2H: broadband V/U shape calls)  
518 of the cryptic myotis at 2,484 m (45.04795, 6.93273, near Colle Lauson, Salbertrand, Torino), in a  
519 landscape characterized by rock debris, alpine prairie and sporadic small larches.

520 We verified the occurrence of the species at further high elevation sites. Observations included  
521 recordings of echolocation calls (FM calls with bandwidth spanning from about 120 to 15 kHz),  
522 sometimes accompanied by social calls, at 2,320 m (45.02270, 6.89885, near Colle Costapiana, Sauze  
523 d'Oulx, Torino; August 2022) and 2,185 m (45.07203, 7.05419, near Colle delle Finestre, Meana di  
524 Susa, Torino; August 2022), and a capture at 2,165 m (44.94676, 6.90607, Diga del Chisonetto,  
525 Sestriere, Torino; one male; 19 September 2018).

527 A mating roost at 2,000 m (45.77747, 6.86673, near Rifugio Combal, Courmayeur, Aosta), consisting  
528 of two small barracks, was surveyed through captures and acoustic recordings in September 2012 and  
529 2013 (Patriarca and Debernardi 2021 supplemented). The highest hibernaculum known is a mine  
530 gallery at 1,670 m (45.69673, 7.63538, mines of Hèrin, Champdepraz, Aosta) (Patriarca and  
531 Debernardi 2021 supplemented).

532 For the sake of completeness, we should mention an old literature record referred to a roosting site  
533 whose elevation is similar to that of our highest acoustic recordings: Amelio and Bonzano (1986)  
534 collected a complete skull, identified as *M. nattereri*, inside the cave Abisso dei Caproschi (44.18819,  
535 7.77915, Magliano Alpi, Cuneo), at 2,419 m (based on the regional speleological database; at 2,435  
536 m according the two authors). Afterwards, citing Amelio and Bonzano (1986), Lanza (2012) wrote  
537 that the skull was recent. Nevertheless, there are actually no remarks about the dating of the skull in  
538 Amelio and Bonzano (1986). Similarly, to our best knowledge there is no information about the dating  
539 of another skull collected in a cave at 2,150 m (44.16641, 7.79069, Abisso C-1 di Monte Rotondo,  
540 Ormea, Cuneo) on 26 September 1971 (Amelio 1973), which Sindaco et al. (1992) considered as  
541 evidence that the cave is used by the species to hibernate.

#### 542 *Myotis daubentonii*

543 The previous elevational record was reported by Toffoli (2017), who captured a male Daubenton's  
544 bat at 2,050 m (Rifugio Miriam, Formazza, Verbano-Cusio-Ossola) on 5 August 2009.

545 We repeatedly recorded the typical walking stick shaped social calls of this species at four lakes  
546 located at higher elevation, inside the Mont Avic Natural Park: at 2,564 m (45.63962, 7.54858, Lago  
547 Gran Betassa IX, Champdepraz, Aosta), where the sequence of calls shown as an example (Fig. 2I)  
548 was recorded on 6 September 2022; at 2,520 m (45.63962, 7.54858, Lago Gran Betassa I,  
549 Champdepraz, Aosta; September 2022, August 2024), 2,289 m (45.62476, 7.57209, Lago Raty  
550 Superiore, Champorcher, Aosta; September 2022, August 2024), and 2,145 m (45.63376, 7.59257,  
551 Lago Vernouille, Champorcher, Aosta; August 2023, August and September 2024, September 2025).  
552 At all these sites, the social calls were interspersed among numerous sequences of echolocation calls  
553 and feeding buzzes, which demonstrate that the species intensively uses these lakes to forage.

554 The highest swarming sites known are the caves Grotta della Brignola (44.20499, 7.77184, Magliano  
555 Alpi, Cuneo) and Rem del Ghiaccio (44.18862, 7.90124, Garessio, Cuneo), where two females were  
556 captured on 26 August 2016 and 20 September 2016 respectively (Toffoli 2017). The elevation of the  
557 two sites, reported at 2,022 and 1,946 m in the paper, should be corrected as 2,045 m and 1,930 m  
558 respectively based on the speleological database.

560 Since swarming sites are often also used by bats in winter, it is possible that the two former caves  
561 also play the role of hibernacula. Hibernating individuals are irregularly found in a cave at 1,530 m  
562 (44.69907, 7.14612, Grotta di Rio Martino, Crissolo, Cuneo); the more recent observations took place  
563 during winter 2024/2025 (Patriarca et al. 2019; Toffoli 2019; Rossi 2025).

564 Amelio and Bonzano (1986) reported the finding of two skulls (identified as *Myotis nathalinae* in the  
565 paper) in two caves at 2,201 m (44.19136, 7.77920, Grotta Excalibur, Magliano Alpi, Cuneo) and  
566 2,150 m (44.16641, 7.79069, Abisso C-1 di Monte Rotondo, Ormea, Cuneo), but the skulls were not  
567 dated.

### 568 *Myotis emarginatus*

569 The elevational record for Geoffroy's bat relates to an individual photographed in a cave at 1,964 m  
570 (44.19141, 7.84775, Buco Fantozzi, Ormea, Cuneo) on 17 August 2017 (Lana et al. 2019).

571 In the autumn swarming phase, two individuals were captured at the entrance of a cave at 1,930 m  
572 (44.18862, 7.90124, Rem del Ghiaccio, Garessio, Cuneo) on 20 September 2016 (Chirosphera 2016;  
573 Zerbetto 2017) and a further one was mistnetted at a mine gallery at 1,670 m (45.69673, 7.63538,  
574 mines of Hérin, Champdepraz, Aosta) on 27 August 2020 (Patriarca and Debernardi 2021  
575 supplemented).

576 Hibernating individuals are sometimes observed in a cave at 1,558 m (44.15148, 7.75133, Grotta  
577 delle Vene, Ormea, Cuneo), where the last observations published occurred on 30 December 2016  
578 (Lana et al. 2021), and are regularly observed in a cave at 1,530 m (44.69907, 7.14612, Grotta di Rio  
579 Martino, Crissolo, Cuneo). The latter is used also as autumn swarming site and for day roosting in  
580 spring and summer (Patriarca et al. 2019; Toffoli 2019; Rossi 2025).

### 581 *Myotis mystacinus*

582 The previous elevational record corresponded to a site at 2,292 m (45.46018, 7.13382, near Lago  
583 Serrù, Ceresole Reale, Torino), where a male and a female were mistnetted on 12 August 2015  
584 (Patriarca et al. 2018 supplemented). We captured other whiskered bats at other similar or higher  
585 elevations: 2,396 m (45.42761, 7.18159, Lago di Nel, Ceresole Reale, Torino; one male; 22 August  
586 2024), 2,368 m (45.47739, 7.28092, Lago inferiore di Ciamousseretto, Noasca, Torino; one male; 23  
587 August 2024), 2,291 m (44.77461, 7.06096, Giardino Alpino Peyronel, Bobbio Pellice, Torino; three  
588 males; 3–4 August 2024), 2,268 m (45.66233, 7.44908, near Lago Layet, Saint-Marcel, Aosta; one  
589 male; 19 July 2020), and 2,115 m (45.41402, 7.22732, near Lago Dres, Ceresole Reale, Torino; one  
590 male and one female; 22 July 2025).

592 Moreover, we recorded some social calls that we identified as probably belonging to this species for  
593 the similarity to some literature descriptions: V-shapes with a duration of about 20 ms and FM calls  
594 ending with a small QCF part (cf. Russ 2021) were recorded at 2,773 m (45.46682, 7.20968, Lago  
595 Lillet, Ceresole Reale, Torino; 10 August 2025) (figs 1J, 1K), 2,526 m (45.48622, 7.14619, Lago  
596 Nivolet Inferiore, Valsavarenche, Aosta; August 2025), and 2,320 m (45.02270, 6.89885, near Colle  
597 Costapiana, Sauze d'Oulx, Torino; August 2022), while four-component FM calls of about 30 ms  
598 (cf. Middleton et al. 2022) were recorded at 2,475 m (45.44305, 7.13432, Alpe Rocce Piccole,  
599 Ceresole Reale, Torino; August 2024). *Myotis brandtii*, which can emit similar calls, is thought to be  
600 absent at these sites, having been recorded only at a great distance from them (see above).  
601 Nevertheless, due to the limited knowledge of the social calls of these and other species of the genus  
602 *Myotis*, we cannot attribute these acoustic data to *M. mystacinus* with absolute certainty.

603 The highest roosting site currently known is a cave at 2,126 m (45.62722, 7.93738, Grotta La Breccia,  
604 Pollone, BI), where one individual was observed in the summer of 2007 (Balestrieri and Sella 2016).  
605 During the autumn swarming period, on 1 September 2024, we captured two male whiskered bats  
606 entering a cave at 2,045 m (44.20499, 7.77184, Grotta della Brignola, Magliano Alpi, Cuneo). The  
607 highest known hibernaculum is a mine at 1,903 m (45.67931, 7.44917, mines of Praborna, Saint-  
608 Marcel, Aosta), where we observed an individual on 1 January 2025.

609 The historical data reported by Amelio and Bonzano (1986) for the caves Abisso dei Caprosci (given  
610 at 2,435 m in the paper, but at 2,419 m according to the regional speleological database; 44.18819,  
611 7.77915, Magliano Alpi, Cuneo) and Abisso C-1 di Monte Rotondo (situated at 2,150 m; 44.16641,  
612 7.79069, Ormea, Cuneo) were based on the finding of two undated skulls. Lanza (2012) wrote that  
613 the skull of Abisso dei Caprosci was recent, but in the cited paper the authors write of fresh remains  
614 only when referring to other species and sites.

#### 615 *Myotis* spp.

616 Between 2022 and 2025 we performed acoustic surveys at sites located higher than the maximum  
617 elevations recorded above for each *Myotis* species. We regularly recorded acoustic activity due to  
618 genus *Myotis*, including feeding buzzes, up to 2,988 m (45.50638, 7.32398, Lago della Losa, Noasca,  
619 Torino; September 2023). Because of the problematic identification of the echolocation calls of these  
620 bats, we could not reach any definitive conclusion about the species involved. Other notable  
621 recordings took place at: 2,840 m (45.48988, 7.26691, Lago superiore di Ciamousseretto, Noasca,  
622 Torino; August and September 2023), 2,827 m (45.46655, 7.21506, near Lago Lillet, Ceresole Reale,  
623 Torino; August 2025), 2,805 m (45.47208, 7.18766, Lago Gias di Beu, Ceresole Reale, Torino; July  
624 and August 2024), 2,773 m (45.46682, 7.20968, Lago Lillet, Ceresole Reale, Torino; July, August

626 and September 2025), and 2,747 m (45.50773, 7.15189, Lago Leynir, Valsavarenche, Aosta;  
627 September 2022, August 2023, July and August 2024, August and September 2025).

### 628 *Nyctalus lasiopterus*

629 The only previous information on the occurrence of *N. lasiopterus* in Piedmont was obtained on 16  
630 October 2021, when an individual fitted with a GPS-GSM tracker in Russia was located near the Po  
631 River at an elevation of 120 m (Vasenkov et al. 2023 supplemented). The bat had covered the longest  
632 movement ever recorded for a bat species (2,515 km), but due to battery depletion, its subsequent  
633 movements remained unknown. Since the individual was a juvenile male, it was suggested that the  
634 movement might have represented a dispersal flight (Russo et al. 2024b).

635 On 8 September 2022, we recorded a sequence of echolocation calls with characteristics attributable  
636 to this species (Fig. 2L: slightly alternating QCF calls with FmaxE of 14.1–14.7 and 14.9–16 kHz,  
637 BL 1.5–3.5, EF 13.1–15.2, dur 14–30 ms, mean dur 24 ms, IPI 570–1700 ms, mean IPI 936 ms) at an  
638 elevation of 2,484 m (45.04795, 6.93273, near Colle Lauson, Salbertrand, Torino). The recording  
639 site, located on the watershed ridge between the Susa and Chisone valleys, is characterized by rocky  
640 debris, alpine meadows, and scattered small larches.

### 641 *Nyctalus leisleri*

642 The previous elevational record was recorded at 2,610 m (45.66597, 7.54992, near Lac Gelé,  
643 Champdepraz, Aosta) on 7 September 2021, during the autumn migration period (Patriarca and  
644 Debernardi 2021 supplemented).

645 In August and September 2024, we recorded echolocation calls emitted by Leisler's bats (e.g., Fig.  
646 2M: QCF calls with FmaxE of 23.5 kHz alternating with calls of FmaxE around 24 kHz) at 2,853 m  
647 (45.47245, 7.19421, near Lago Gias di Beu, Ceresole Reale, Torino), in a landscape characterised by  
648 rock debris. Moreover, we recorded acoustic sequences similarly attributable to this species (QCF  
649 calls with FmaxE of 22.6–24.5kHz alternating with calls of higher FmaxE and slightly broader  
650 bandwidth) at the following other elevations above the maximum previously recorded: 2,839 m  
651 (45.48988, 7.26691, Lago Superiore di Ciamousseretto, Noasca, Torino; September 2023), 2,805 m  
652 (45.47208, 7.18766, Lago Gias di Beu, Ceresole Reale, Torino; August 2024), 2,749 m (45.51409,  
653 7.16105, near Pian Borgnoz, Valsavarenche, Aosta; September 2024), 2,737 m (45.50212, 7.14768,  
654 Laghi Trebecchi, Valsavarenche, Aosta; August and September 2024), and 2,703 m (45.49367,  
655 7.13216, Lago Leità, Ceresole Reale, Torino; September 2022).

656 At some sites the echolocation calls, often accompanied by feeding buzzes, were recorded throughout  
657 summer, demonstrating that this species uses the alpine pastures of the study area as foraging ground

659 outside migration periods. These recordings took place at 2,520 m (45.63962, 7.54858, Lago Gran  
660 Betassa I, Champdepraz, Aosta; September 2022, July and August 2024, August 2025), 2482 m  
661 (45.47760, 7.27510, Lago inferiore di Ciamousseretto, Noasca, Torino; July and August 2023), and  
662 2,435 m (45.07136, 6.95578, near Colle dell'Assietta, Exilles, Torino; July, August, and September  
663 2022). The majority of the recordings were nonetheless taken in late summer/early autumn,  
664 suggesting that they were at least partially due to migrating bats. During the same period we recorded  
665 echolocation sequences probably emitted by this species (since it is far more common than  
666 acoustically similar species in the area) even at higher elevations, but, due to the lower frequency of  
667 the lower calls (FmaxE of 20–22.5 kHz) or to the absence of a clear frequency alternation, we  
668 conservatively identify them just as “probable”. One of these sequences (QCF calls with FmaxE of  
669 22 kHz irregularly alternating with QCF calls with broader bandwidth and FmaxE around 24.2 kHz,  
670 IPI 300–1568 ms, dur 8.9–11.6 ms) was recorded at 3,065 m (45.49497, 7.33134, Colle dei Becchi,  
671 Locana, Torino; August 2023), which is the highest elevation that we surveyed.

672 We recorded feeding buzzes up to 2,805 m (45.47208, 7.18766, Lago Gias di Beu, Ceresole Reale,  
673 Torino; August 2024) and captured some individuals at 2,291 m (44.77461, 7.06096, Giardino Alpino  
674 Peyronel, Bobbio Pellice, Torino; two males; 3 August 2024), 1,925 m (45.06412, 7.03067, Lago  
675 delle Rane, Usseaux, Torino; one male; 11 August 2023), and 1,776 (44.74761, 7.07984, near Rifugio  
676 B. Lowrie, Bobbio Pellice, Torino; one female and six males; 2–3 September 2024).

677 *N. leisleri* largely uses the study area to mate. Possibly because of the difficulty of detecting its  
678 occurrence in winter, there are no data about hibernation sites.

### 679 *Nyctalus noctula*

680 This species is uncommon in the Italian Western Alps. Previous published data on its occurrence  
681 were scarce, limited to elevations below 1,000 m (Sindaco et al. 1992; Debernardi and Patriarca  
682 2007), and lacking for the Aosta Valley (Patriarca and Debernardi 2021). However, in this very  
683 region, on 18 August 2025 we recorded echolocation calls emitted by this species (Fig. 2N: QCF  
684 calls, FmaxE 18.6–20.9 kHz, EF 17.6–19.7 kHz, BL 1–1.7 kHz, dur 16.3–17 ms) at 2,520 m  
685 (45.63962, 7.54858, Lago Gran Betassa I, Champdepraz, Aosta), on a glacial lake surrounded by rock  
686 debris. We recorded further echolocation calls (QCF calls with FmaxE of 17.5–19.9 kHz alternated  
687 with FM-QCF calls with higher FmaxE) at various sites in the valleys of Susa, Chisone and Pellice:  
688 at 2,435 m (45.07136, 6.95578, near Colle dell'Assietta, Exilles, Torino; August 2022), 2,412 m  
689 (44.98746, 6.86787, near Colle Basset, Sestriere, Torino; August 2022), 2,185 m (45.07203, 7.05419,  
690 near Colle delle Finestre, Meana di Susa, Torino; August 2022), and 1,776 m (44,74761, 7,07984,  
691 near Rifugio B. Lowrie, Bobbio Pellice, Torino; September 2024).

693 Given the recording period, the above mentioned calls may have been emitted by migrating  
694 individuals. However, at a site situated at 1,310 m (45.17775, 7.38327, Colle Lys, Viù, Torino), we  
695 ascertained through acoustic recording and captures the uninterrupted occurrence of common  
696 noctules from March to September 2022, although we do not know if during the breeding season this  
697 was limited to males.

698 Possibly because of the difficulty of detecting the species in winter, there are no data about its  
699 hibernation sites in the study area.

#### 700 *Pipistrellus kuhlii*

701 The elevational record is reported in the literature and relates to the recording of social calls at 2,208  
702 m (45.86133, 7.15964, Casa Carioni, Saint-Rhémy-En-Bosses, Aosta), which took place on 27  
703 August 2016 (Caprio et al. 2020). We recorded analogous social calls at lower elevation sites, the  
704 highest of which are situated at 2,145 m (45.63376, 7.59257, Lago Vernouille, Champorcher, Aosta;  
705 August 2023, August 2024, July 2025), 2,124 m (44.89055, 7.13070, Conca Cialancia Natural Park,  
706 Perrero, Torino; July 2018), and 1,925 m (45.06412, 7.03067, Lago delle Rane, Usseaux, Torino;  
707 August 2023).

708 Information about the roost sites in which this species hibernates is scarce and limited to elevations  
709 below 1,000 m.

#### 710 *Pipistrellus nathusii*

711 The highest site for which the complex social song of *P. nathusii* has been reported is situated at  
712 1,582 m (45.82338, 7.17840, Frazione Bosses, Saint-Rhemy-en-Bosses, Aosta); the recording was  
713 collected on 14 September 2016 (Caprio et al. 2020). Even if we have not recorded social calls at  
714 higher elevation, we are confident in attributing to this migratory and fairly cold-tolerant species an  
715 echolocation sequence composed of rarefied QCF calls (Fig. 20: FmaxE 39.5 kHz, BL 0.5 kHz, IPI  
716 500–550 ms) that we recorded at 2,610 m (45.66597, 7.54992, near Lac Gelé, Champdepraz, Aosta)  
717 on 7 September 2021. The period and the elevation make an association with a sedentary and  
718 thermophilous species such as *P. kuhlii* unlikely. The recording site is characterised by rock outcrops,  
719 patches of alpine prairie and small lakes.

720 During winter, some individuals have been found in piles of wood at sites below 1,000 m.

#### 721 *P. kuhlii/P. nathusii*

722 We recorded echolocation calls attributable to *P. kuhlii/P. nathusii* at the following notable  
723 elevations: 2,564 m (45.63962, 7.54858, Lago Gran Betassa IX, Champdepraz, Aosta; August 2023

725 and 2024), 2,526 m (45.48622, 7.14619, Lago Nivolet Inferiore, Valsavarenche, Aosta; September  
726 2022 and August 2024), 2,520 m (45.63962, 7.54858, Lago Gran Betassa I, Champdepraz, Aosta;  
727 August 2024), 2,484 m (45.04795, 6.93273, near Colle Lauson, Salbertrand, Torino; August,  
728 September, and October 2022), 2,443 m (45.46671, 7.15237, Casotto PNGP di Bastalon, Ceresole  
729 Reale, Torino; September 2024), 2,435 m (45.07136, 6.95578, near Colle dell'Assietta, Exilles,  
730 Torino; August, September, and October 2022), 2,412 m (44.98746, 6.86787, near Colle Basset,  
731 Sestriere, Torino; August, September, and October 2022), 2,403 m (45.47075, 7.25615, Alpe di  
732 Breuil, Noasca, Torino; September 2025), 2,390 m (45.60008, 7.44574, near Alpe Tsavanis, Cogne,  
733 Aosta; September 2021), 2,347 m (45.03791, 6.91427, near Colle Blegier, Oulx, Torino; August,  
734 September, and October 2022), and 2,320 m (45.02270, 6.89885, near Colle Costapiana, Sauze  
735 d'Oulx, Torino; August 2022).

### 736 *Pipistrellus pipistrellus*

737 This is one of the most common bats in the Italian western Alps, perhaps the most common of all.  
738 The previous elevational record reported in literature was 2,610 m (45.66597, 7.54992, near Lac Gelé,  
739 Champdepraz, Aosta) (Patriarca and Debernardi 2021).

740 We recorded the common pipistrelle almost everywhere we performed acoustic surveys, including at  
741 a site wholly occupied by rock debris, at 3,046 m (45.48861, 7.25431, Colle della Torre, Noasca,  
742 Torino). An example of the echolocation calls recorded at this site is the sequence in figure 1P (QCF  
743 calls, mean FmaxE 47.4 kHz, BL 1.1 kHz), which was recorded on 22 August 2023.

744 Other notable recordings took place at 2,853 m (45.47245, 7.19421, near Lago Gias di Beu, Ceresole  
745 Reale, Torino; August 2024), 2,839 m (45.48988, 7.26691, Lago Superiore di Ciamousseretto,  
746 Noasca, Torino; June and August 2023), 2,827 m (45.46655, 7.21506, near Lago Lillet, Ceresole  
747 Reale, Torino; July, August, September 2025), 2,749 m (45.51409, 7.16105, near Pian Borgnoz,  
748 Valsavarenche, Aosta; August 2024), 2,747 m (45.50773, 7.15189, Lago Leynir, Valsavarenche,  
749 Aosta; August 2023 and 2024), 2,737 m (45.50212, 7.14768, Laghi Trebecchi, Valsavarenche, Aosta;  
750 August 2024), and 2,703 m (45.49367, 7.13216, Lago Leità, Ceresole Reale, Torino; September 2022,  
751 August 2023, July and August 2024, August and September 2025). We recorded feeding buzzes up  
752 to 2,853 m (45.47245, 7.19421, near Lago Gias di Beu, Ceresole Reale, Torino; August 2024).

753 Some hibernating individuals identified as *P. pipistrellus*/*P. pygmaeus*, but probably belonging to this  
754 species (since it is far more common than *P. pygmaeus* in the study area) are irregularly observed in  
755 two caves situated at 1,558 m (44.15148, 7.75133, Grotta delle Vene, Ormea, Cuneo) and 1,530 m  
756 (44.69907, 7.14612, Grotta di Rio Martino, Crissolo, Cuneo). The last published observations at these

two sites occurred on 30 December 2016 (Lana et al. 2021) and 2 February 2018 (Patriarca et al. 2019), respectively.

### *Pipistrellus pygmaeus*

The previous elevational record was due to echolocation calls recorded at 1,911 m (45.67440, 7.45001, near Alpe Mulac, Saint-Marcel, Aosta) on 4 September 2020 (Patriarca and Debernardi 2021 supplemented).

We recorded an echolocation sequence of this species (Fig. 2Q: QCF calls, FmaxE 53.7 kHz, SF 54.4 kHz, EF 53.9 kHz, dur 6.7 ms) at 2,526 m (45.48622, 7.14619, Lago Nivolet Inferiore, Valsavarenche, Aosta) on 29 August 2024. Another sequence, in all probability due to the soprano pipistrelle (QCF calls, FmaxE 52.3 kHz, SF 52.9 kHz, EF 52.8 kHz, dur 7.3 ms), was recorded at 2,412 m (44.98746, 6.86787, near Colle Basset, Sestriere, Torino) on 21 August 2022.

There is no information regarding the highest hibernacula. The winter observations of individuals that could belong to this species (sightings, not supported by criteria of sure specific identification) should be referred to the *P. pipistrellus*/*P. pygmaeus* pair and, as observed above, are more probably due to *P. pipistrellus*.

### *Plecotus auritus*

Two individuals—a male and a lactating female—were captured over a pond at 2,402 m (45.59670, 7.46001, Alpe Broillot, Cogne, Aosta) on 09 July 2020; their identification was confirmed through genetic analysis (Patriarca and Debernardi 2021 supplemented). The record is not only noteworthy for the elevation of the site, but also because it was collected in an open habitat type—an alpine pasture—unusual for this species, which is described as a primarily forest bat.

During summer, we captured brown long-eared bats at 2,292 m (45.46018, 7.13382, near Lago Serrù, Ceresole Reale, Torino; one male, identification genetically confirmed; 12 August 2015) and 2,070 m (45.68719, 7.34039, Comboè Inferiore, Charvensod, Aosta; five females and five males, for a female and a male identification was genetically confirmed; 25 July 2020). A further individual was captured at 2,100 m (45.61702, 7.55486, near Dondenaz, Champorcher, Aosta; one male; 4 August 2011) (A. Alberdi and I. Garin, pers. comm.).

Individuals have been captured at various swarming underground sites, the highest of which is a cave at 2,045 m (44.20499, 7.77184, Grotta della Brignola, Magliano Alpi, Cuneo), where we mistnetted two males on 1 September 2024.

Old literature reports some other data associated with high elevations. Amelio and Bonzano (1986) reported the finding of two skulls that were found covered by debris in the cave Abisso dei Caproschi

(44.18819, 7.77915, Magliano Alpi, Cuneo; situated at 2,435 m according to the paper, yet at 2,419 m based on the regional speleological database). Lanza (2012) wrote that the two skulls were recent and considered the elevation of the site as the highest recorded for *P. auritus*, but, to our best knowledge, the remains were actually undated, thus this record cannot be taken into consideration. Amelio and Bonzano (1986) also reported the measurements of some fresh skulls, but these were collected at other sites. Two of them, dating to 1978 and 1979, were found at 2,253 m (at “about 2,300 m” according to Amelio and Bonzano 1986) in the cave Lambda-15 del Mongioie (44.18016, 7.78293, Magliano Alpi, Cuneo) and other 61 skulls, said to be at least partially fresh by Calandri (1976), were collected in the early 1970s at 2,150 m, in the cave Abisso C-1 di Monte Rotondo (44.16641, 7.79069, Ormea, Cuneo). The skulls of both sites were referred to *P. auritus* by Amelio and Bozano (1986), but those of Abisso C-1 di Monte Rotondo were cited in other literature sources as belonging to *P. austriacus* (Amelio 1973; Calandri 1976; Bologna and Vigna Taglianti 1985; Sindaco et al. 1992), or mentioned as data of both *P. auritus* and *P. austriacus* (Agnelli 2006). Amelio and Bonzano (1986) reported the values of maximum diameter of the tympanic bulla and length of the mandibular tooth row for one of the two skulls of the cave Lambda-15 and for 15 skulls of the cave Abisso C1 of Monte Rotondo. These measurements fall within the ranges proposed by Blant et al. (2008) to identify *P. auritus* and, with only one exception, are either consistent with the values referred by Benda and Ivanova (2003) to *P. auritus* or are even smaller, and thus equally attributable to *P. auritus* (this species features values of the two biometrics smaller than those of *P. macrobullaris* and *P. austriacus*). The exception is represented by one of the skulls of the cave Abisso C-1, whose measurements fall within those proposed by Benda and Ivanova (2003) for *P. macrobullaris*. Despite the limitations of cranial morphological analysis in the identification of *Plecotus* species (Andriollo and Ruedi 2018), the values observed allow us to exclude the attribution of the skulls to *P. austriacus*, are consistent with the identification of at least part of the skulls as *P. auritus*, and do not exclude a possible occurrence in the sample of *P. macrobullaris*.

### *Plecotus austriacus*

This species has not been recorded in the Aosta Valley (Patriarca and Debernardi 2021) and is probably rare and localised in Piedmont.

Godio et al. (2022) reported the finding of a dead individual inside a building at Zuccaro (Valduggia, Vercelli) on 17 June 2021. The recording site is located on the foothills of the Alpine chain (lower Valsesia), at an elevation of 630 m, which is the highest recorded for this species in the study area. The specimen was identified based on morphological traits (M. Cucco, pers. comm.).

824 The grey long-eared bat certainly occurs across the Northern Apennines chain, which extends into  
825 the south-eastern sector of the study area. Hibernating individuals have been observed in an  
826 abandoned hydroelectric dam at 290 m (44.56880, 8.61504, Bric Zerbino dam, Molare, Alessandria)  
827 (data provided by Ente di gestione Aree protette Appennino piemontese) and in a complex of mine  
828 galleries (Ferriere, Casaleggio Boiro, Alessandria) whose entrances open between 340 and 510 m,  
829 although the source reporting these data (Biggi et al. 2011) does not specify in which galleries and  
830 when the observations exactly took place. Grey long-eared bats are reported to use some of these  
831 mines also for day roosting (Toffoli 2011).

832 The data reported by Sindaco et al. (1992), which include older observations, are questionable. In  
833 particular, those referred to the sites situated above the current elevational record cannot be taken into  
834 consideration for the following reasons: an observation for the elevation of 2,230 m, with reference  
835 to the cave C-25 of Monte Rotondo (Ormea, Cuneo; not included in the speleological database) is  
836 wrong because the original source concerned a *Myotis (Selysius)* and not a *Plecotus* bat (Calandri  
837 1976); the occurrence in the cave Carsna d'Aie (synonym Carsena dell'Agnello or Grotta C-29,  
838 Ormea, Cuneo), located at 2,300 m according to the paper, but at 2,200 according to the speleological  
839 database (which does not report the coordinates of the site) was reported following the finding of  
840 "remains" identified as *P. austriacus* by Calandri (1976) prior to the description of *P. macrobullaris*  
841 and without specifying the identification criteria; the data for the cave Abisso C1 of Monte Rotondo,  
842 situated at 2,150 m (44.16641, 7.79069, Ormea, Cuneo) relate to the finding, in the early 1970s, of  
843 skulls that were later attributed by Amelio and Bonzano (1986) to *P. auritus* and that, based on the  
844 biometrics reported by the two authors, are not attributable to *P. austriacus* (see what exposed above  
845 regarding *P. auritus*); the specimen collected at 810 m (Ponte di Nava, Ormea, Cuneo) in 1947 and  
846 preserved in the Milan Natural History Museum is recorded in the museum catalogue as a *P. auritus*.

#### 847 *Plecotus macrobullaris*

848 Forty-nine males and three females of this species were captured at 2,292 m (45.46018, 7.13382, near  
849 Lago Serrù, Ceresole Reale, Torino) on 12 August 2015. All these individuals featured the typical  
850 triangular chin pad of the species; moreover, the identification of four of them was further validated  
851 genetically (Patriarca et al. 2018 supplemented). Other individuals were captured at 2,100 m  
852 (45.61702, 7.55486, near Dondenaz, Champorcher, Aosta; three males; 4 August 2011) (A. Alberdi  
853 and I. Garin, pers. comm.), 2,060 m (44.88712, 7.12357, near Lago Lauson, Perrero, Torino; one  
854 male; 19 July 2018) (our data), and 1,978 m (45.46091, 7.14867, near Alpe Brangie, Ceresole Reale,  
855 Torino; six males; 24 June 2015) (Patriarca et al. 2018 supplemented).

857 We collected some fresh droppings belonging to the species, identified through DNA barcoding, in a  
858 World War II bunker at 2,290 m (45.065918, 6.660203, Batteria B3 delle Quattro Sorelle,  
859 Bardonecchia, Torino; October 2025).

860 The highest autumn swarming site where the occurrence of *P. macrobullaris* has been reported  
861 (following captures in 2016) is a cave at 1,930 m (44.18862, 7.90124, Rem del Ghiaccio, Gressio,  
862 Cuneo) (Zerbetto 2017).

### 863 *P. auritus/P. macrobullaris*

864 The previous elevational record of genus *Plecotus* was recorded at 2,610 m (45.66597, 7.54992, near  
865 Lac Gelé, Champdepraz, Aosta) (Patriarca and Debernardi 2021 supplemented).

866 We recorded echolocation calls emitted by *Plecotus* bats up to 3,065 m (45.49497, 7.33134, Colle dei  
867 Becchi, Locana, Torino; recorded on 17 September 2023), which is the highest elevation that we  
868 surveyed. Other notable recordings took place at 2,853 m (45.47245, 7.19421, near Lago Gias di Beu,  
869 Ceresole Reale, Torino; July, August and September 2024), 2,773 m (45.46682, 7.20968, Lago Lillet,  
870 Ceresole Reale, Torino; August and September 2025), 2,749 m (45.51409, 7.16105, near Pian  
871 Borgnoz, Valsavarenche, Aosta; August 2024), 2,747 m (45.50773, 7.15189, Lago Leynir,  
872 Valsavarenche, Aosta; July 2024, August 2025), 2,737 m (45.50212, 7.14768, Laghi Trebecchi,  
873 Valsavarenche, Aosta; July and August 2024), and 2,703 m (45.49367, 7.13216, Lago Leità, Ceresole  
874 Reale, Torino; September 2022, July and August 2024, July and August 2025).

875 Current identification criteria are insufficient to distinguish these calls at the species level;  
876 nevertheless, given that the few occurrences of *P. austriacus* reported for the study area are limited  
877 to distant and ecologically different sites (see above), their possible attribution must be restricted to  
878 the *P. auritus/P. macrobullaris* acoustic pair.

879 The same identification applies to the hibernating long-eared bats recorded in the inner sectors of the  
880 Alpine valleys of the study area. Individuals are irregularly observed at various underground sites,  
881 the highest of which are a fortification at 1,880 m (45.049487, 7.048512, Forte Serre Marie,  
882 Fenestrelle, Torino) and a wartime gallery at 1,690 m (45.04764, 6.87858; Opera 276, Oulx, Torino),  
883 where we observed single individuals on 11 February 2024 and on 27 February 2024 respectively.  
884 Hibernating individuals are also reported for a cave at 1,530 m (44.69907, 7.14612; Grotta di Rio  
885 Martino, Crissolo, Cuneo), where the last observations published occurred in the winter 2014/2015  
886 (Toffoli 2019).

### 887 *Vespertilio murinus*

889 The previous elevational record was based on the capture of a male at 2,402 m (45.59670, 7.46001;  
890 Alpe Broillot, Cogne, Aosta) on 9 July 2020 (Patriarca and Debernardi 2021 supplemented). The  
891 same literature source reported a capture at 1,965 m (45.82241, 7.61953, Col Pilaz, La Magdeleine,  
892 Aosta; one male; 7 August 2020) and the recording of social calls at 2,258 m (45.63876, 7.49921;  
893 Val Clavalité, Fénis, Aosta; July 2021).

894 On 31 August 2024, near a lake surrounded by alpine meadows and rocky debris, we recorded a  
895 sequence of social calls attributable to this species (Fig. 2R: sigmoid calls with FmaxE around 12–14  
896 kHz, corresponding to the QCF portion) at 2,526 m (45.48622, 7.14619; Lago Nivolet Inferiore,  
897 Valsavarenche, Aosta), which corresponds to the current elevational record. We recorded further  
898 social calls at 2110 m (45.074708, 6.673123, Punta Tre Croci, Bardonecchia, Turin; July 2025) and  
899 captured the species at 2,291 m (44.77461, 7.06096; Giardino Alpino Peyronel, Bobbio Pellice, Turin;  
900 one male; 3 August 2024).

901 It is not known if this species reproduces or hibernates in the study area.

## 902 Overall results

903 In the study area, we identified new elevational records for 15 bat species and obtained records for  
904 the remaining 14 species by reviewing the literature (Tab. 2; Fig. 3). Most records (55.2%) resulted  
905 from acoustic surveys; the others were obtained through roost inspections or captures (27.6%), mist-  
906 netting of foraging or commuting individuals (13.8%), and, in one case, the incidental discovery of a  
907 dead specimen (3.4%). All elevational records were obtained during summer, with the exception of  
908 those for *R. ferrumequinum* and *R. euryale*, which were recorded during winter.

909 The difficulty of contacting or reliably identifying some bat species using acoustic methods has  
910 hindered the possibility to determine the maximum elevation they reach, as can also be inferred by  
911 considering the elevational records detected for species groups. Those observed for the groups  
912 *Eptesicus/Nyctalus/Vespertilio*, *M. blythii/M. myotis*, *Myotis* spp., and *P. auritus/P. macrobullaris* are  
913 higher than those of any individually identified species belonging to these assemblages.  
914 Consequently, at least one species within each group occurs at the highest elevation documented for  
915 the group.

916 The elevational record observed for the group *P. pipistrellus/M. schreibersii/P. pygmaeus*, which is  
917 higher than the records identified for *M. schreibersii* and *P. pygmaeus*, but lower than that ascertained  
918 for *P. pipistrellus*, highlights a possible occurrence of *M. schreibersii* and *P. pygmaeus* at higher  
919 elevations. The record itself may, however, refer to *P. pipistrellus*.

920 Lastly, it is important to note that the highest elevation where we recorded bats (the groups  
921 *Eptesicus/Nyctalus/Vespertilio* and *P. auritus/P. macrobullaris*) correspond to the highest elevation

923 that we surveyed (3,065 m); therefore, we cannot exclude occurrences of these or other bats at even  
924 higher sites.

925 As a whole, the bats recorded at the highest elevations (above 2,800 m) are: *T. teniotis*, *H. savii*, at  
926 least one species of the genus *Myotis* (considering the characteristics of the social calls recorded at  
927 2,703 m, probably *M. mystacinus*), *N. leisleri*, *P. pipistrellus*, and at least one species of the *P.*  
928 *auritus/P. macrobullaris* pair. *Barbastella barbastellus* and *E. nilssonii* (recorded above 2,700 m),  
929 and *P. nathusii* (above 2,600 m) follow next.

930 By reviewing the literature, we found some data from surveys carried out in the 1960s–1980s in caves  
931 above 2,100 m that have not been resurveyed in recent years. Being old and mainly based on undated  
932 skeletal remains, such data could not be considered of current value. The elevations of those caves  
933 are higher than those of the sites where the species once associated with them have been observed  
934 roosting in recent years; however, current elevations records for most of these species (mainly  
935 obtained through acoustic surveys) are similar or even higher, so we cannot rule out the possibility  
936 that those caves are still used today. Because of this, it would be worth it to survey them once again.

## 937 DISCUSSION

### 938 Comparison with elevational records collected at national and international level

939 The bat elevational records observed in our study area constitute a first checklist of this type of data  
940 for Italy and, for most species, they represent the highest documented in the country.

941 In its monograph on Italian bats, regarding the 29 species of our study area, Lanza (2012) mentions  
942 elevational records mainly recorded in countries other than Italy. Those he reports for Italian locations  
943 are sometimes questionable, since they concern findings of undated remains (as stated above with  
944 respect to some skulls found in caves), or lower than the upper elevations at which we have recorded  
945 the same species in our study area. The only two exceptions are an elevational record of *M. capaccinii*  
946 (1,484 m, Monti Lessini, Verona) originated from the finding of a skull assessed as recent (Vernier  
947 2011) and a supposed record of *M. mystacinus* (2,680 m, in Lombardy) that cannot be considered  
948 valid because it does not appear in the putative source of the information (Zilio and Fornasari 2001).  
949 Similarly, the recently published *Atlas of Mammals in Italy* (Loy et al. 2025) is of little use for  
950 comparisons with our elevational records. The data included in the Atlas were often recorded as  
951 corresponding to the centroids of the 10×10 km geographical cells in which they were collected (data  
952 obtained from the 2013–2019 report under Article 17 of the Habitats Directive) or to the elevations  
953 of nearby toponyms (as is the case for part of the data sourced from the CKmap database; Latella et  
954 al. 2006). In the Alps, where elevation can vary greatly over short distances, such values may differ

956 substantially from the actual elevations of the observation sites. Moreover, in the bat species accounts,  
957 the authors often reported elevational records taken from across each species' global range, and only  
958 for *E. nilssonii* and *M. capaccinii* they specify that the cited elevational records refer to observations  
959 in Italy. For *E. nilssonii*, the Atlas reports foraging individuals up to 2,600 m (Ladurner and Panizza  
960 2025), an elevation lower than the upper limit recorded in our study area, while for *M. capaccinii* it  
961 cites the aforementioned record by Vernier (2011) approximated at an elevation of 1,500 m (Lapini  
962 and Calvini 2025 supplemented), which is higher than that of the only site where we recorded *M.*  
963 *capaccinii* in our study area.

964 The low elevation at which we observed *M. capaccinii* is unsurprising, since the study area lies at the  
965 northern edge of this species' range. For similar reasons, the upper elevations reached in our study  
966 area by other species that are locally rare can be expected to be exceeded in Italian regions where  
967 these species are far more common. By consulting colleagues and grey literature, we established that  
968 this is certainly the case for *R. euryale*, *P. austriacus*, and *M. schreibersii* in peninsular Italy. Based  
969 on heterodyne acoustic surveys carried out in 1997, the occurrence of *R. euryale* was reported for a  
970 cave at 1,390 m in Umbria (Bani et al. 2000), where its presence needs to be reassessed due to the  
971 time elapsed and the touristification of the site. Afterwards, in Abruzzo, acoustic data attributed to  
972 this species were recorded at 1,595 in the period 2013–2016 (Ferri et al. 2018) and at 1,059 m in 2019  
973 (Ente Parco Nazionale d'Abruzzo, Lazio e Molise 2022). For *P. austriacus*, recent unpublished data—  
974 obtained through direct observation and measurement of individuals—were recorded at 1,388 m in  
975 Tuscany (G. Dondini, S. Vergari, pers. comm.) and at 1,460 m in Calabria (P.P. De Pasquale, pers.  
976 comm.). The occurrence of *M. schreibersii* has been reported based on acoustic surveys carried out  
977 in Abruzzo at about 1,600 m (Ferri et al. 2013) and, during 2025, at 1,880 m (F. Roscioni, pers.  
978 comm.).

979 We cannot exclude the existence of other data from local sources—which may be difficult to access—  
980 reporting elevations higher than those we recorded. That said, except for *M. schreibersii*, *R. euryale*,  
981 *M. capaccinii*, and *P. austriacus*, to the best of our knowledge, the elevational records identified in  
982 our study area represent the highest documented so far for bats in Italy.

983 For 14 species—*B. barbastellus*, *M. bechsteinii*, *M. crypticus*, *M. daubentonii*, *M. emarginatus*, *M.*  
984 *mystacinus*, *N. lasiopterus*, *N. leisleri*, *N. noctula*, *P. kuhlii*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus*,  
985 and *P. auritus*—the elevational records of our study area are also higher than those reported for the  
986 species' global ranges in the IUCN species accounts (accessed on 20/12/2025) and in the *Handbook*  
987 *of the mammals of the world* (Wilson and Mittermeier 2019). On the other hand, relating to Europe,  
988 in the *Handbook of the mammals of Europe* (Russo 2023) three of these species—*M. bechsteinii*, *M.*  
989 *emarginatus*, and *P. nathusii*—are respectively associated with the following higher elevations: 1,650

991 m (Petrov 2006; Reiter et al. 2013), 2,200 m (Dietz and Pir 2023), and 3,100 m (Hargreaves et al.  
992 2017).

993 Higher elevational records for 10 of the 14 species listed above can be found in some works that  
994 consider bat occurrence at a local level. *Myotis bechsteinii*, *M. emarginatus*, *M. mystacinus*, and *P.*  
995 *auritus* have been recently reported for a cave situated at 2,600 m in Bulgaria, where the bats were  
996 captured during autumn swarming (Dundarova and Popov 2024). In the French Alps, *N. lasiopterus*  
997 was acoustically detected at 2,811 m (Dumont and Colombo 2024). *Nyctalus leisleri*, *P. nathusii*, *P.*  
998 *pipistrellus*, and *P. pygmaeus* were acoustically recorded at the extraordinary elevation of 3,460 m in  
999 the Swiss Alps (Zingg and Bontadina 2016; Zingg et al. 2022). Similarly, in the Austrian Alps,  
1000 acoustic contacts with *N. leisleri*, *N. noctula*, *P. nathusii*, and *P. pipistrellus* were recorded at 3,106  
1001 m, and some sequences of *P. pygmaeus* at 2,906 m (Widerin and Reiter 2018). On the other hand, in  
1002 the same area, the highest observations for genera *Myotis* and *Plecotus* (Widerin and Reiter 2017,  
1003 2018) occurred at elevations 470 m and 547 m lower, respectively, than those we recorded in our  
1004 study area.

1005 To our best knowledge, the highest elevations observed in our study area for the remaining four  
1006 species—*B. barbastellus*, *M. crypticus*, *M. daubentonii*, and *P. kuhlii*—are worldwide records.

### 1007 **Factors and reasons underlying bat occurrence at high elevations**

1008 The presence of bats at high elevation is likely facilitated by organisms' abilities such as cold  
1009 tolerance, the capacity to fly even under moderately windy conditions, the ability to cover  
1010 considerable distances quickly (thus allowing them to exploit sites that are far apart within the same  
1011 night and/or to pass rapidly through unsuitable areas), and the ability to forage in open environments.  
1012 Most of the species that we recorded above 2,300 m (the natural tree-line limit on western Italian  
1013 Alps; Ozenda 1985) are cold-tolerant bats, as demonstrated by their ranges, which reach or extend  
1014 further north than 60 degrees of latitude. According to the distribution maps shown in Russo (2023),  
1015 this applies to *E. nilssonii*, *M. daubentonii*, *M. mystacinus*, *N. noctula*, *P. nathusii*, *P. pipistrellus*, *P.*  
1016 *pygmaeus*, *P. auritus*, and *V. murinus*. Other bats that occur beyond the same parallel are *M. nattereri*,  
1017 whose sibling species *M. crypticus* occurs in the study area above 2,300 m, and *M. brandtii*, whose  
1018 rarity in the study area has negatively affected the probability to identify the highest elevation it  
1019 reaches.

1020 Species belonging to the genera *Nyctalus*, *Tadarida*, and *Vespertilio* show adaptations to fast,  
1021 enduring flight (e.g., the long and narrow wings) and *Nyctalus/Vespertilio* have been found to be less  
1022 sensitive to low/moderate wind speeds compared to other bats (Behr et al. 2017).

1024 Another species we recorded at high elevation—*H. savii*—although it does not possess the same fast-  
1025 flight capability as the previous species, is nonetheless highly capable of flight in open environments  
1026 (Kipson et al. 2023). Moreover, it should be remembered that other bats, apparently less suited to  
1027 open supra-forest habitats, may still frequent them by flying close to the ground (in this way they find  
1028 some shelter from the wind and, presumably, in the absence of vertical structural references, they use  
1029 the ground itself as a reference). This behavior has been described for *P. macrobullaris*, *M. nattereri*  
1030 complex, and *M. myotis* (Alberdi et al. 2013).

1031 Several reasons may explain the presence of bat species at high elevation, including the possibility to  
1032 shorten movements following straight routes (as suggested by detections at mountain passes, e.g.,  
1033 Oppliger 2004), the availability of potential roosts (such as crevices in rock walls and interstices or  
1034 larger spaces in screes and blockfields, BRHK 2022), and foraging opportunities, which may be  
1035 granted by the seasonal bursts of local prey during the short summer (e.g., Knop et al. 2023) and/or  
1036 the occurrence of swarms of high-flying arthropods (including actively migrants, e.g., (Dreyer et al.  
1037 2018), and passively transported species, (e.g., Heiniger 1989).

1038 Regarding seasonal movements, we observe that some of the elevational records that we collected  
1039 are most likely due to latitudinally migrating individuals. Indeed, the seasonal period of many  
1040 observations is consistent with transits of the four bats—*N. leisleri*, *N. noctula*, *P. nathusii*, and *V.*  
1041 *murinus*—which are well known for migrating over long distances (Hutterer et al. 2005). As of *N.*  
1042 *noctula*, it is noteworthy that its highest recording site in our study area is situated in Aosta Valley,  
1043 where the occurrence of this species was formerly unknown (Patriarca and Debernardi 2021). From  
1044 2023, during late summer we recorded some other echolocation sequences of this species along the  
1045 valley bottom of this region.

1046 Taking into account that *P. pygmaeus* is rather rare in the study area, its elevational record—collected  
1047 at the end of August—adds some evidence in support of the hypothesis that this species, whose  
1048 seasonal movements are poorly known (Hutterer et al. 2005), may also have migratory habits. The  
1049 few acoustic detections of its occurrence at very high elevation reported for the Swiss (Zingg et al.  
1050 2022) and the Austrian Alps (Widerin and Reiter 2018) were recorded in late summer or autumn as  
1051 well. *Pipistrellus pygmaeus* has been described as not adapted to perform long flights in straight line  
1052 (Froidevaux et al. 2023), yet it has proved capable of some long-distance movements, which are also  
1053 suggested by patterns of genetic structure (Jones and Froidevaux 2023).

1054 The month during which we recorded *N. lasiopterus* (September) suggests that the individual  
1055 recorded might have been migrating as well. However, it is equally possible that it belonged to a  
1056 resident French population of this species and was detected during a daily movement. The recording  
1057 site is located 40 km from a site in France—not farther than 700 m from the Italian border—where the

1059 greater noctule has been recorded (Dumont and Colombo 2024). Such a distance can easily be  
1060 covered by this species (Popa-Lisseanu et al. 2009; Nad'ò et al. 2019). In any case, the record confirms  
1061 the occurrence of the species in Piedmont.

1062 Similarly, not all the occurrences of the above-mentioned migratory species can be attributed to  
1063 latitudinally migratory events. Data collected in the early summer demonstrate that at least *N. leisleri*  
1064 and *V. murinus*, among these species, are present in the study area up to 2,400–2,500 m also outside  
1065 migration periods, possibly attracted by foraging opportunities. *N. leisleri* could be attracted to high-  
1066 elevation sites by the availability of insects associated with cattle dung, which have been reported to  
1067 be important prey for this bat in pasture areas in England and Ireland (Shiel et al. 1998). Potential  
1068 prey available on the water bodies within the study area, and widely used by both *N. leisleri* and *V.*  
1069 *murinus*, include various insects with aquatic larvae (Ephemeroptera, Trichoptera,  
1070 Chironomidae/Ceratopogonidae, Culicidae) (Shiel et al. 1998; Safi and Jaberg 2021).

1071 *Tadarida teniotis* is highly adapted to fast flying (O'Mara et al. 2021); however, it is generally  
1072 considered a non-migratory bat (Hutterer et al. 2005). The many high elevation data that we recorded  
1073 for it are consistent with the local availability of cliffs with rock crevices, which may be used to roost  
1074 by this species, and the occurrence of migratory fluxes of the medium-large moths (Menz et al. 2022)  
1075 that often constitute the bulk of its diet (Amorim et al. 2023). A significant correlation between the  
1076 acoustic activity of this species and numbers of migrating insects has been found in the Pyrenees  
1077 (Hawkes et al. 2023).

1078 Roosting and foraging opportunities, together with a high degree of ecological plasticity, can also  
1079 explain the occurrence at extreme elevations of *P. pipistrellus* and *H. savii*, which are species very  
1080 common in the Alps of the study area (e.g., Toffoli et al. 2016; Patriarca and Debernardi 2021).

1081 On the contrary, the contacts with *B. barbastellus* recorded above 2,700 m might appear surprising,  
1082 since this species is considered a typical forest bat (e.g., Meschede and Heller 2003). Nonetheless, it  
1083 has colonized non-forest landscapes in central and southern Italy (Ancillotto et al. 2014, 2015),  
1084 demonstrating some degree of ecological flexibility. *Barbastella barbastellus* is considered mostly a  
1085 sedentary species, although some remarkable movements (up to 290 km) have been recorded  
1086 (Hutterer et al. 2005). Our repeated observations of its occurrence at high elevation could be explained  
1087 by seasonal movements (possibly migratory), and/or by an ecological adaptation to use structurally  
1088 non-optimal open habitat types, which may become attractive during the occurrence of swarms of  
1089 migrating moths. Flows of migrating noctuid moths, known to be preyed upon by *B. barbastellus*  
1090 (Zeale et al. 2011; Carr et al. 2020), have been reported at the Gran San Bernardo pass (Hachler et al.  
1091 2002), where the barbastelle was also detected at high elevation (Caprio et al. 2020). However, a  
1092 study conducted at a mountain pass in the Pyrenees found that activity levels of this species in

1094 September were not influenced by the abundance of nocturnally migrating insects, and suggested that  
1095 *B. barbastellus* used the pass to move between different foraging areas or while searching for  
1096 hibernacula (Hawkes et al. 2023).

1097 Considering the literature on another moth specialist –*P. macrobullaris*– and primarily the works  
1098 carried out in the Pyrenees, which highlight the importance of high elevation sites as roosting and  
1099 foraging ground for this species (Alberdi et al. 2012, 2015), it seems very probable that it reaches  
1100 much higher elevations than those ascertained up to now in our study area. In the Pyrenees, mountain  
1101 long-eared bats, including a lactating female, have been captured at 2,800 m (Alberdi et al. 2013). As  
1102 already stated above, we recorded echolocation calls attributable to the acoustic pair *P. auritus*/*P.*  
1103 *macrobullaris* up to 3,065 m, which suggest that the elevational range of *P. macrobullaris* reported  
1104 for the Alpine chain by Alberdi et al. (2013) was biased downwards due to scarce sampling effort.  
1105 However, we must also note that the capture of a lactating female of *P. auritus*, occurred at 2,402 m  
1106 in our study area, demonstrates that this species too, despite being usually associated with woodland  
1107 (Razgour et al. 2011; Ancillotto and Russo 2023), can forage at least occasionally in open habitat  
1108 types of high elevation, and that this can take place even during biological phases of strong energetic  
1109 demand.

1110 Similarly, favourable foraging opportunities—particularly the abundance of midges (Tiberti et al.  
1111 2016)—are likely to explain the intense activity of *M. daubentonii* recorded over some alpine lakes  
1112 in the study area. It should be noted that, given the high abundance of glacial lakes, the need for  
1113 drinking cannot account for the bat activity observed at these sites, unlike what happens at lower  
1114 elevations, where the scarcity of lakes and of other calm water bodies leads to bat aggregations  
1115 associated with drinking.

1116 Some of the above-mentioned reasons for the presence of bats at high elevation may act  
1117 synergistically, e.g., migrating bats can take advantage of foraging opportunities, including the food  
1118 source represented by migrating insect flows (Hawkes et al. 2023). Finally, we note that climatic  
1119 conditions, together with the temporal availability of (and competition for) food resources and the  
1120 location of important roosts, potentially represent the drivers of elevational migration, a phenomenon  
1121 that is still scarcely investigated in bats (McGuire and Boyle 2013).

### 1122 **Implications for conservation**

1123 The observation of many bat species and of their activity patterns at elevations higher than those  
1124 previously known has important conservation implications. These concern both the mitigation of local  
1125 environmental impacts, and the study and mitigation of global impacts, particularly those related to  
1126 climate change.

1128 Regarding local impacts, our results highlight the need to explicitly consider bats when assessing the  
1129 consequences of human activities in high-elevation areas. This applies, for instance, to the  
1130 construction of tourist infrastructures that may cause important environmental alterations (e.g., ski  
1131 facilities; Negro et al. 2010), and to the building of high-elevation energy plants, including wind  
1132 farms and dams (Bontadina et al. 2014). In particular, wind turbines, which can cause fatal collisions  
1133 with bats, are being increasingly installed in the Alpine landscape at elevations close to or above the  
1134 timberline. For example, not far from our study area, wind farms have been built near the San  
1135 Gottardo Pass and the Nufenen Pass (Switzerland) at elevations of approximately 2,100–2,500 m,  
1136 and an additional project near the Gran San Bernardo Pass is currently pending judgment by the Swiss  
1137 Federal Court. Advances in technology may enable wind energy development at even higher  
1138 elevations, as demonstrated by the Nanshan Cuomei County Zhegu wind farm in Tibet, which  
1139 operates at elevations exceeding 5,000 m. Bats that migrate and/or fly high above the ground can be  
1140 severely impacted by wind farm mortality, yet operational curtailment to reduce this threat is seldom  
1141 implemented (Voigt et al. 2022). Moreover, the adaptation of some species to the harsh climate of  
1142 high mountains probably calls for even stricter curtailment than at lower elevations, due to the  
1143 probable differences in the influence of temperature and wind speed on bat activity and the resulting  
1144 collision risk. In addition, wind farms, as well as dams or other lighted infrastructures and buildings,  
1145 can also introduce artificial light into otherwise dark landscapes, affecting bats and their prey  
1146 (Patriarca et al. 2018) which are highly sensitive to light pollution (e.g., Bennie et al. 2018; Boyes et  
1147 al. 2021).

1148 Beyond hazardous infrastructures, human activities can also interact with bat populations in more  
1149 subtle, indirect ways. For example, the introduction of fish into naturally fishless Alpine lakes is  
1150 known to reduce the availability of emerging insects, thus potentially decreasing the suitability of  
1151 these lakes as foraging habitats for bats (Gruenstein et al. 2021). Similarly, pastoral activities at high  
1152 elevations can alter habitats, for instance by limiting forest development (presumably to the detriment  
1153 of forest-dwelling bats), or by affecting insect abundance and diversity through overgrazing (Negro  
1154 et al. 2011; Fragnière et al. 2022), with possible consequences for the whole bat community.

1155 Furthermore, our work provides a clear reference for future studies on the effects of climate change  
1156 on Alpine bat populations by offering an up-to-date overview of the elevational records of bats in the  
1157 Alpine region. Among the species surveyed, the thermophilic ones—such as *M. emarginatus*, *P. kuhlii*,  
1158 and the rhinolophids—appear particularly suitable as target species for monitoring the distributional  
1159 shifts along the elevational gradient that may be driven by global warming. As a matter of fact,  
1160 compared to the species we have detected at higher elevations, these have a broader elevational range  
1161 within which to move if temperatures increase. Unfortunately, their limited acoustic detectability has

1163 likely hindered the identification of the maximum elevations they reach, underscoring the need for  
1164 further studies to improve current knowledge.

1165 Lastly, from a conservation perspective, it is worth evidencing that the ability of bats to mitigate the  
1166 effects of climate change through upward distributional shifts depends on the availability of suitable  
1167 high-elevation habitats; consequently, mountainous regions such as our study area may act as climatic  
1168 refugia supporting the long-term conservation of some bat populations.

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## 1188 Statements and Declarations

1189 **Conflict of Interest.** Not Applicable.

1190 **Data availability.** All data generated or analysed during this study are included in this published  
1191 article and its supplemental information files.

1192 **Animal Ethics.** The captures of bats carried out by the authors were authorized by the Italian Ministry  
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1196 0008882/PNM del 08/05/2014 Div II, mamte.PNM.REGISTRO.UFFICIALE.U.0007303.07-04-  
1197 2017, m amte.MITE.REGISTRO.UFFICIALE.USCITA.00566210.06/05/2022, m  
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**Table 1. Survey effort according to method and elevation.**

<b>Elevational range (m a.s.l.)</b>	<b>N bat detector nights</b>	<b>N capture nights</b>	<b>N captured bats</b>	<b>N inspected roost</b>
0-1000	1614	69	595	479
1000-2000	1101	59	559	115
> 2000	1096	14	39	19

**Table 2. Elevational records of bats (in bold) in the study area.**

All data were collected from 2005 onwards, except for three records which are older. There are reasons to consider these older records still valid today: the mountain areas where they were obtained have not undergone significant environmental changes (e.g., expansion of built-up areas, infrastructure development, or other major land-use changes) in recent decades, and climate warming is expected to increase rather than decrease elevational records. However, given the long time elapsed since the collection of the oldest record (for *M. blythii*), we prefer not to include it among the current records; nevertheless, it differs only slightly from the most recent record.

Sector= area where the record was detected. Alps are classified according to the International Standardized Mountain Subdivision (Marazzi, 2005), as shown in fig. 1.

\* The Pennine Alps border the Piedmont sector of Lake Maggiore where the recording site is located.

Year= most recent year of known occurrence of the species/species group at the recording site.

\*\* Record collected on an unspecified date between 1991 and 2002.

Taxa	Elevation (m a.s.l.)	Sector	Survey method	Year	Data source
<b>Miniopteridae</b>					
<i>Miniopterus schreibersii</i>	<b>1555</b>	Apennine	Acoustic	2022	Toffoli 2025
<b>Molossidae</b>					
<i>Tadarida teniotis</i>	<b>3046</b>	Graian Alps	Acoustic	2023	Present study
<b>Rhinolophidae</b>					
<i>Rhinolophus euryale</i>	<b>1030</b>	Ligurian Alps	Roost (capture, inspection)	2012	Patriarca et al. 2012
<i>Rhinolophus ferrumequinum</i>	1801	Cottian Alps	Acoustic	2024	Present study
	<b>1947</b>	Ligurian Alps	Roost (inspection)	1998	Pascutto and Balestrieri 2000
<i>Rhinolophus hipposideros</i>	1760	Ligurian Alps	Roost (inspection)	2019	Lana et al. 2021
	<b>Ca. 2000</b>	Ligurian Alps	Roost (inspection)	1991/2002**	Toffoli 2005
<b>Vespertilionidae</b>					
<i>Barbastella barbastellus</i>	<b>2703</b>	Graian Alps	Acoustic	2024	Present study
<i>Eptesicus nilssonii</i>	<b>2703</b>	Graian Alps	Acoustic	2024	Present study
<i>Eptesicus serotinus</i>	<b>2275</b>	Cottian Alps	Acoustic	2018	Present study
<i>Hypsignathus savii</i>	<b>2853</b>	Graian Alps	Acoustic	2024	Present study
<i>Myotis bechsteini</i>	<b>1530</b>	Cottian Alps	Roost (capture, IR photo)	2018	Patriarca et al. 2019; Toffoli 2019
<i>Myotis blythii</i>	<b>1930</b>	Ligurian Alps	Roost (capture)	2016	Lana and Balestra 2017
	2000	Maritime Alps	Capture	1987	Sindaco et al. 1992
<i>Myotis myotis</i>	<b>1530</b>	Cottian Alps	Roost (capture)	2010	Toffoli 2019
<i>Myotis blythii/M. myotis</i>	<b>2460</b>	Graian Alps	Acoustic	2015	Patriarca et al. 2018
<i>Myotis brandtii</i>	<b>1827</b>	Lepontine Alps	Capture	2005	Toffoli 2006
<i>Myotis capaccinii</i>	<b>205</b>	Pennine Alps*	Roost (capture, inspection)	2024	Garzoli et al. 2025
<i>Myotis crypticus</i>	<b>2484</b>	Cottian Alps	Acoustic	2022	Present study
<i>Myotis daubentonii</i>	<b>2564</b>	Graian Alps	Acoustic	2024	Present study
<i>Myotis emarginatus</i>	<b>1964</b>	Ligurian Alps	Roost (inspection)	2017	Lana et al. 2019
<i>Myotis mystacinus</i>	<b>2396</b>	Graian Alps	Capture	2024	Present study
<i>Myotis</i> spp.	<b>2988</b>	Graian Alps	Acoustic	2023	Present study
<i>Nyctalus lasiopterus</i>	<b>2484</b>	Cottian Alps	Acoustic	2022	Present study
<i>Nyctalus leisleri</i>	<b>2703</b>	Graian Alps	Acoustic	2023	Present study
<i>Nyctalus noctula</i>	<b>2520</b>	Graian Alps	Acoustic	2025	Present study
<i>Pipistrellus kuhlii</i>	<b>2201</b>	Pennine Alps	Acoustic	2016	Caprio et al. 2020
<i>Pipistrellus nathusii</i>	<b>2610</b>	Graian Alps	Acoustic	2021	Present study
<i>Pipistrellus kuhlii/P. nathusii</i>	<b>2564</b>	Graian Alps	Acoustic	2023	Present study
<i>Pipistrellus pipistrellus</i>	<b>3046</b>	Graian Alps	Acoustic	2023	Present study
<i>Pipistrellus pygmaeus</i>	<b>2526</b>	Graian Alps	Acoustic	2024	Present study
<i>Plecotus auritus</i>	<b>2402</b>	Graian Alps	Capture	2020	Patriarca and Debernardi 2021
<i>Plecotus austriacus</i>	<b>630</b>	Pennine Alps	Found dead	2021	Godio et al. 2022
<i>Plecotus macrobullaris</i>	<b>2292</b>	Graian Alps	Capture	2015	Patriarca et al. 2018
<i>Plecotus auritus/P. macrobullaris</i>	<b>3065</b>	Graian Alps	Acoustic	2023	Present study
<i>Vespertilio murinus</i>	<b>2526</b>	Graian Alps	Acoustic	2024	Present study
<i>Eptesicus/Nyctalus/Vespertilio</i>	<b>3065</b>	Graian Alps	Acoustic	2023	Present study
<b>Miniopteridae/Vespertilionidae</b>					
<i>Min. schr./Pip. pip./Pip. pyg.</i>	<b>2703</b>	Graian Alps	Acoustic	2024	Present study

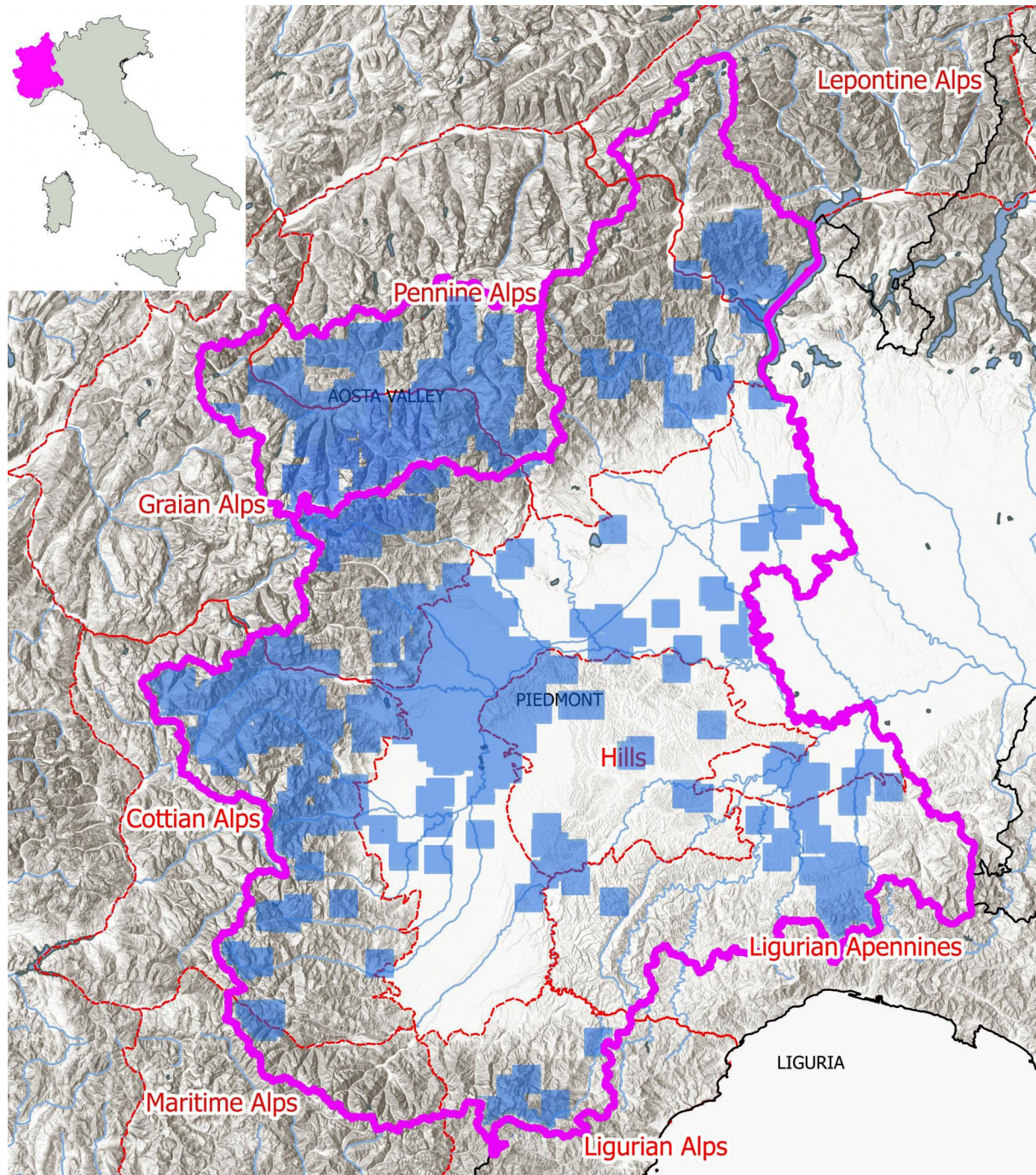
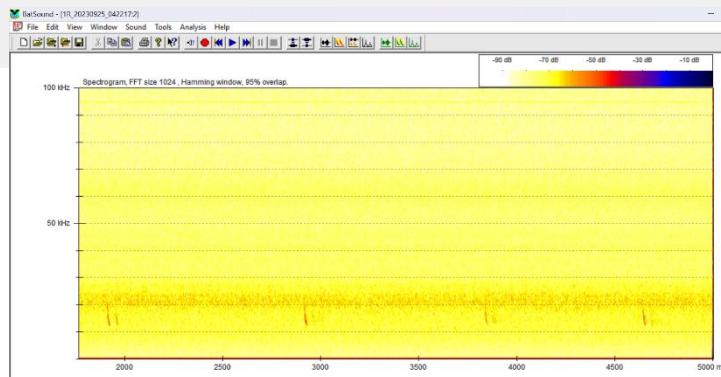


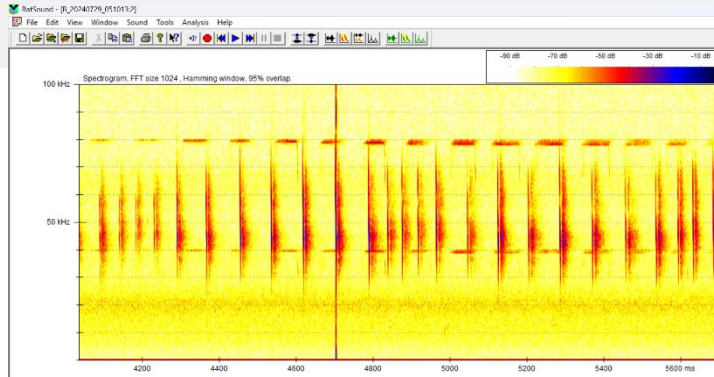
Figure 1. Map of the study area (Piedmont and Aosta Valley) with surveyed sectors (squares).

Figure 2

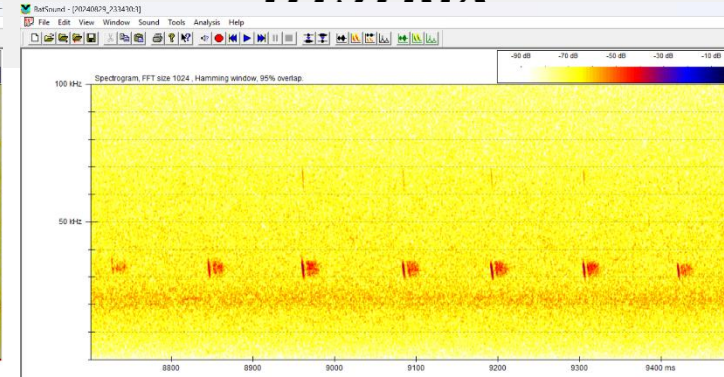
**HYSTRIX**



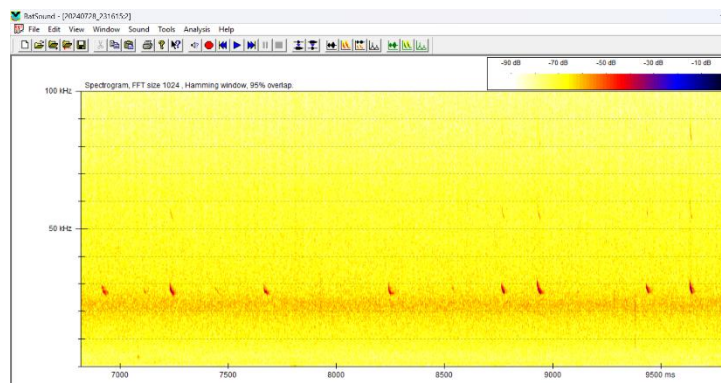
**A, *T. teniotis***



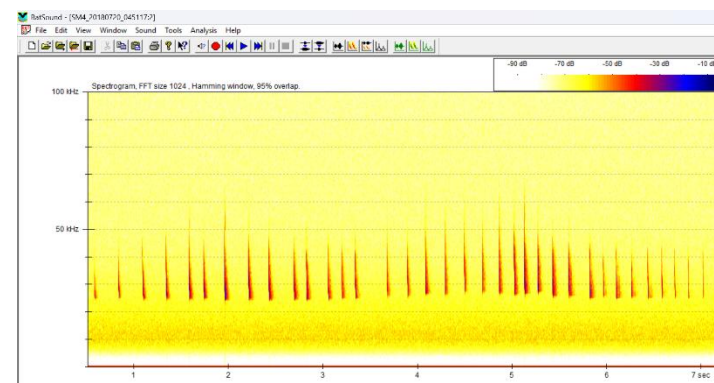
**B, *R. ferrumequinum* (and *Myotis* sp.)**



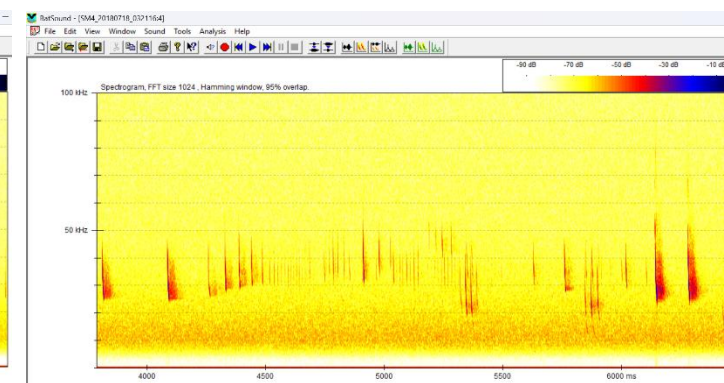
**C, *B. barbastellus***



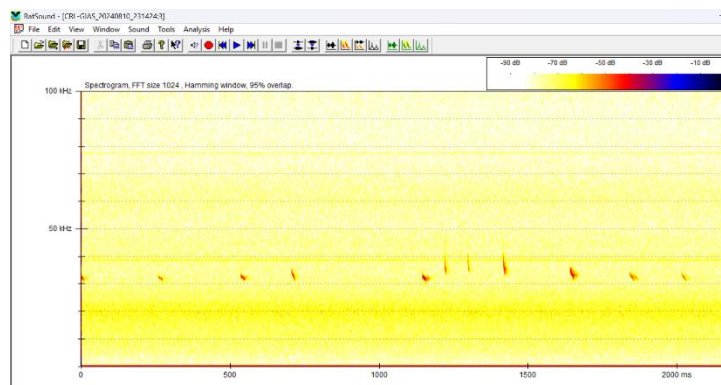
**D, *E. nillssonii***



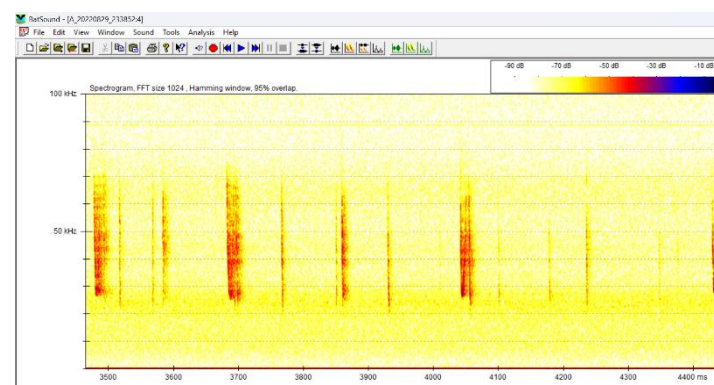
**E, *E. serotinus***



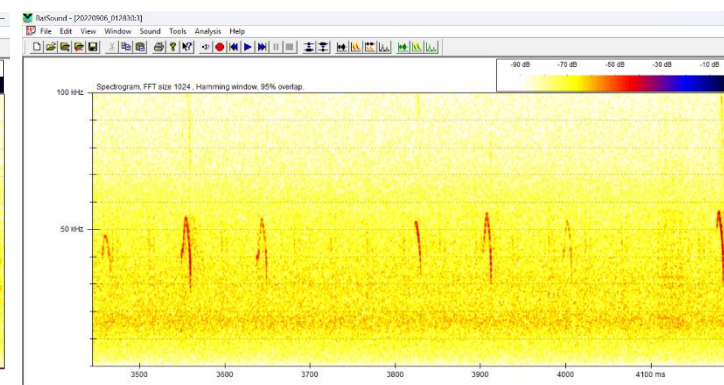
**F, *E. serotinus***



**G, *H. savii***



**H, *M. crypticus***

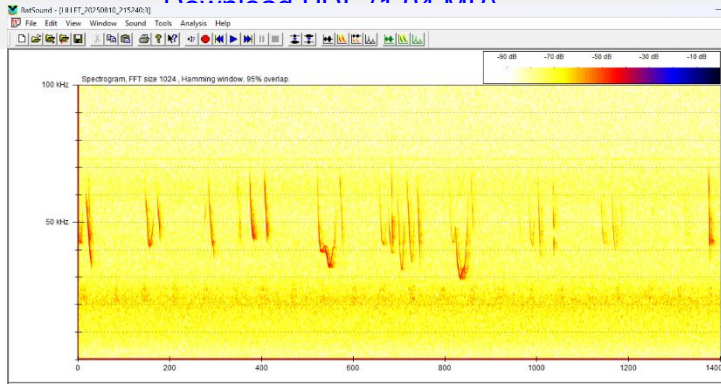


**I, *M. daubentonii***

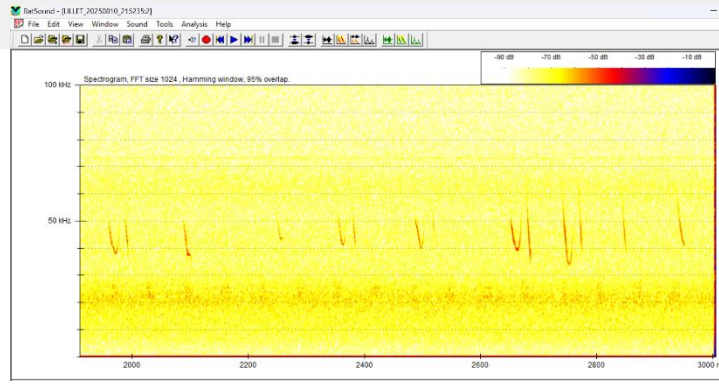
# Figure 2

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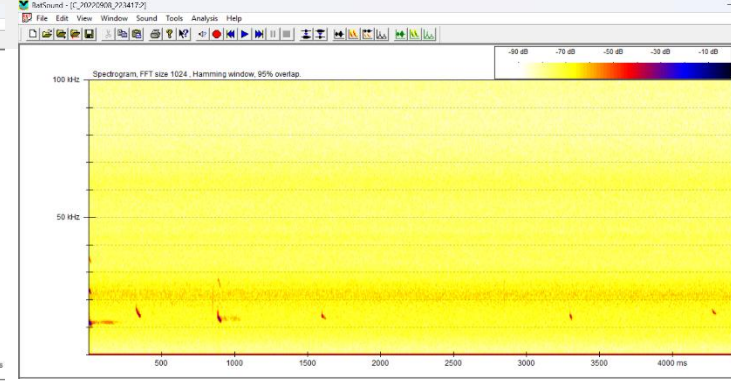
# HYSTRIX



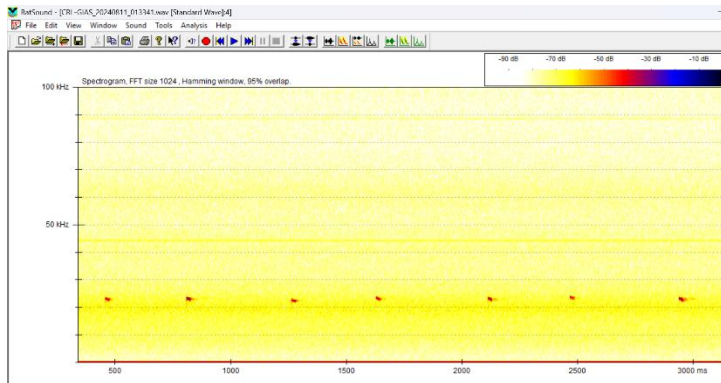
J, probable *M. mystacinus*



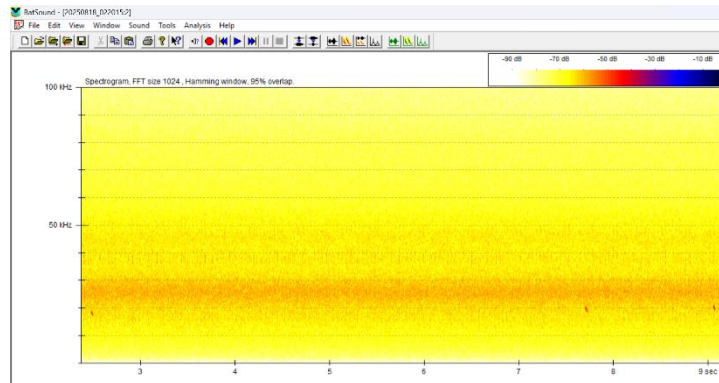
K, probable *M. mystacinus*



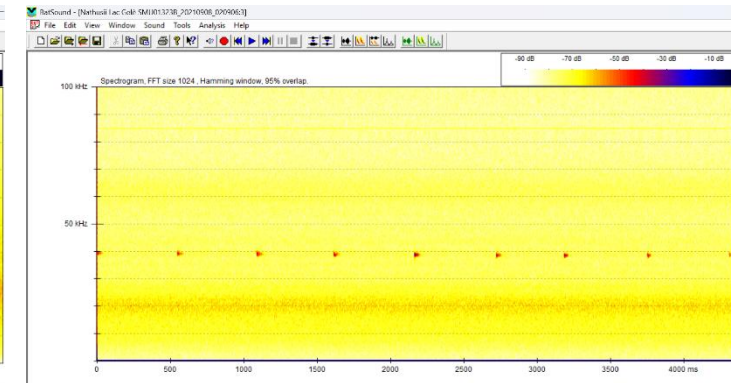
L, *N. lasiopterus*



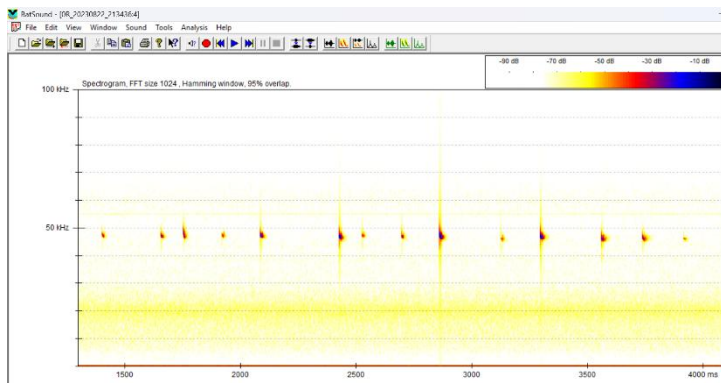
M, *N. leisleri*



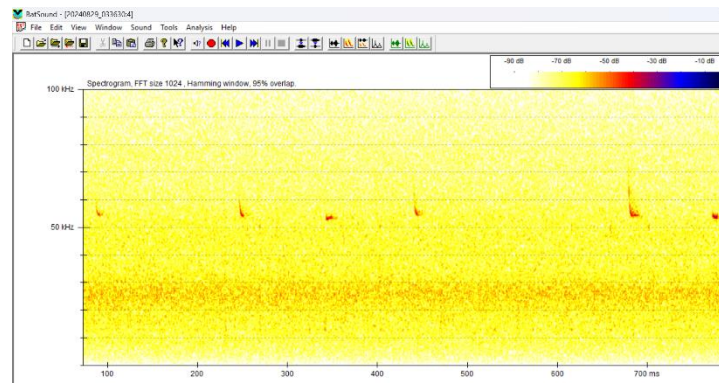
N, *N. noctula*



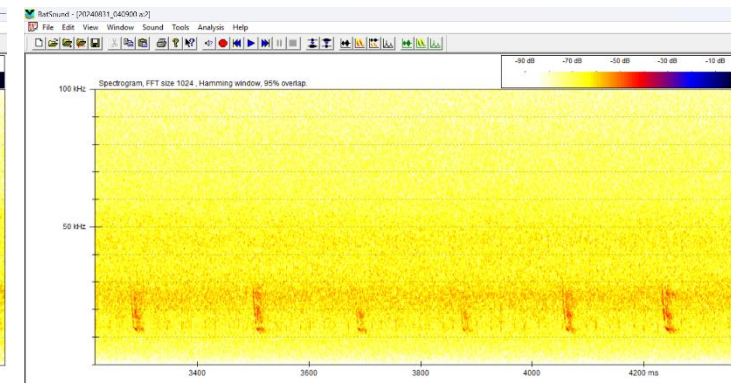
O, *P. nathusii*



P, *P. pipistrellus*



Q, *P. pygmaeus*



R, *V. murinus*

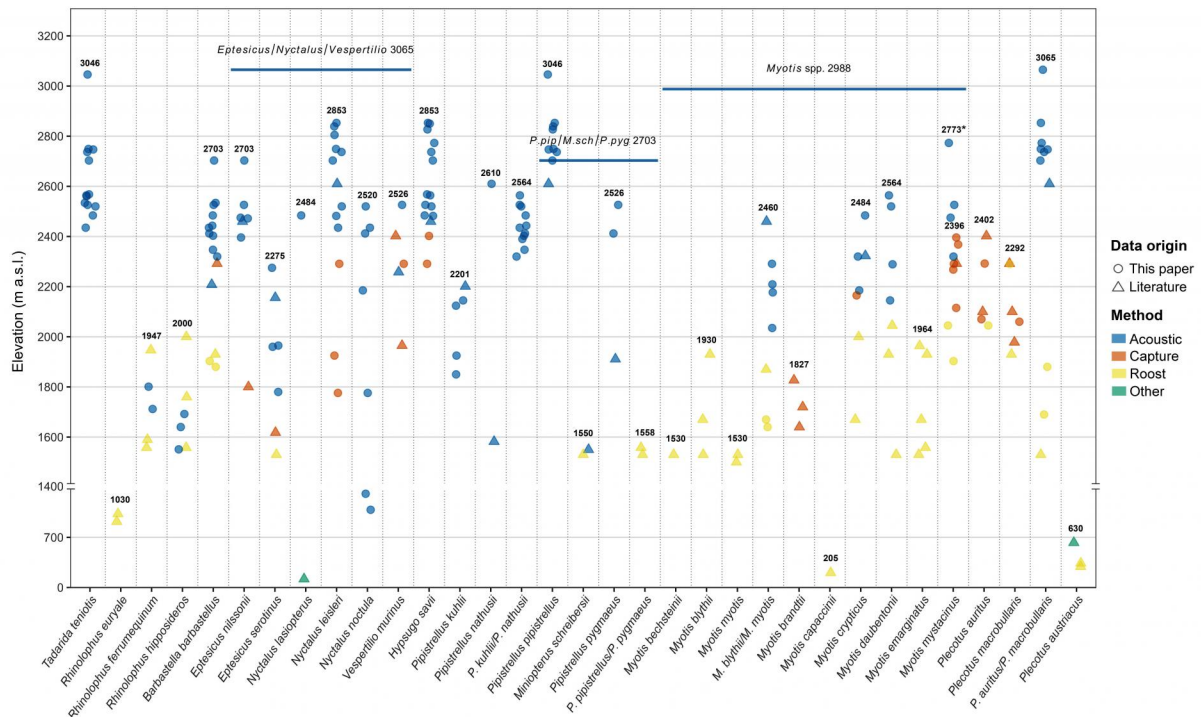


Figure 3. Current data reported in the paper summarized according to their source. Figures show the elevational records. Captures at roost entrances are included under “Roost”. “Other” corresponds to a GPS-GSM fix of a marked individual (*N. lasiopterus*) and to an individual found dead (*P. austriacus*). \*Social calls probably emitted by *M. mystacinus* have been recorded up to 2,773 m; however, due to some uncertainty in their identification, the elevation record of this species should be considered 2,396 m, which corresponds to a capture.

**Manuscript body**

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**Tables**

Table 1 - [Download source file \(14.5 kB\)](#)

Table 1. Survey effort according to method and elevation.

Table 2 - [Download source file \(2.01 MB\)](#)

Table 2. Elevational records of bats (in bold) in the study area.

All data were collected from 2005 onwards, except for three records which are older.

There are reasons to consider these older records still valid today: the mountain areas where they were obtained have not undergone significant environmental changes (e.g., expansion of built-up areas, infrastructure development, or other major land-use changes) in recent decades, and climate warming is expected to increase rather than decrease elevational records. However, given the long time elapsed since the collection of the oldest record (for *M. blythii*), we prefer not to include it among the current records; nevertheless, it differs only slightly from the most recent record.

Sector= area where the record was detected. Alps are classified according to the International Standardized Mountain Subdivision (Marazzi, 2005), as shown in fig. 1.

\* The Pennine Alps border the Piedmont sector of Lake Maggiore where the recording site is located.

Year= most recent year of known occurrence of the species/species group at the recording site.

\*\* Record collected on an unspecified date between 1991 and 2002.

**Figures**

Figure 1 - [Download source file \(10.15 MB\)](#)

Figure 1. Map of the study area (Piedmont and Aosta Valley) with surveyed sectors (squares).

Figure 2 - [Download source file \(1.04 MB\)](#)

Figure 2. Spectrograms of echolocation/social calls corresponding to the species elevational records that we detected through the acoustic method (A, C, D, E, F, G, H, I, L, M, N, O, P, Q, R) and to other notable recordings (B: echolocation calls of *R. ferrumequinum* recorded at the highest site where we acoustically detected this species; K and J: social calls probably emitted by *M. mystacinus*).

Figure 3 - [Download source file \(7.06 MB\)](#)

Figure 3. Current data reported in the paper summarized according to their source.

Figures show the elevational records. Captures at roost entrances are included under "Roost". "Other" corresponds to a GPS-GSM fix of a marked individual (*N. lasiopterus*) and to an individual found dead (*P. austriacus*). \*Social calls probably emitted by *M. mystacinus* have been recorded up to 2,773 m; however, due to some uncertainty in their identification, the elevation record of this species should be considered 2,396 m, which corresponds to a capture.

**Supplementary Online Material**

File 1 - [Download source file \(21.84 kB\)](#)

S1. Molecular protocols for the identification of *Plecotus* spp.

File 2 - [Download source file \(1.63 MB\)](#)

S2. Locations where the data reported in the paper were collected. Unconfirmed old data have not been mapped.