

Effect of climatic and palaeoenvironmental changes on the occurrence of Holocene bats in the Swiss Alps

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Michel Blant,¹ Marco Moretti^{2,3} and Willy Tinner⁴

Abstract

A large-scale palaeozoological study compared 45 ¹⁴C-dated bat remains from the southern and northern Swiss Alps with palaeovegetational and palaeoclimatic data. Four thermophilous (warm-demanding) and four psychrophilous (cold-tolerant) bat species, mainly forest dwellers, were selected for the study. *Myotis blythii* is the oldest bat species recorded in the Alps, i.e. on the southern side, going back to the early Holocene at 10 500 cal. BP. Our study showed that thermophilous species (e.g. *Myotis bechsteinii* and *Rhinolophus hipposideros*) were most abundant during the Holocene climatic optimum in Central Europe (10 000–4000 cal. BP), when warm-demanding mixed forests were dominant. Psychrophilous species such as *Myotis brandtii* also occurred during the climatic optimum, but most of the samples fall into the onset of the late Holocene (Sub-Atlantic period), when summer temperatures were already declining. These species declined in the southern Alps after 4000 cal. BP, when fire was intensively used by humans to convert portions of the forest into open land. This fire practice modified forest species composition and structure, with effects on forest-dwelling bat communities. We conclude that during the early and mid Holocene bat community compositions mainly depended on climate and related vegetation and forest structure dynamics. With increasing land use during the mid and late Holocene, anthropogenic changes of forest composition and creation of open habitats increasingly co-determined bat-population dynamics in the Alps. These Swiss findings are in agreement with previous results from eastern Central Europe.

Keywords

bats, indicators, palaeovegetation, palaeoclimate, radiocarbon dating, Swiss Alps

Introduction

In recent decades palaeoecological studies have increasingly aimed to improve the knowledge of postglacial environmental history and the succession of plant and animal communities. Comprehension of such processes can give important insights on the origin of present environmental and biodiversity patterns, with their relationship being shaped by the legacy of different evolutionary forces. Furthermore, these studies represent a crucial step towards the development of quantitative models forecasting the response of species and communities to current climatic changes (Oldfield and Alverson, 2003; Overpeck *et al.*, 2003).

Most palaeoecological studies have been focusing on plant communities (palaeobotany), especially through the study of pollen (palynology). For animals, classical archeozoological studies consider the environmental reconstruction of settlements of Palaeolithic and Mesolithic hunters and later of Neolithic or younger farmers (e.g. Hüster-Plogmann *et al.*, 1999; Morel and Müller, 1997; Schibler and Jacomet, 1999; Schibler and Stepan, 1999). Studies on the remains of particular faunal indicator species, however, are rare. Interesting perspectives in the use of this approach have been shown by recent analyses carried out on taxa such as Chironomida, Cladocera, Coleoptera, Oribatida, Pisces and Ostracoda in sedimentary layers (e.g. Brooks, 2000; Elias, 2001; Finney *et al.*, 2002; Heiri and Lotter, 2003; Hofmann, 2000; Korhola and Rautio, 2001; Solhoy, 2001). Only a few preliminary attempts, however, have been carried out using small mammals and particularly bats (e.g. Blant *et al.*, 2004; Postawa, 2004) or bat guano deposit (Carbonnel *et al.*, 1999).

Studies of bat populations have been mostly restricted to species distribution analyses without including the temporal components, especially because of systematic problems, such as limited technical tools and the expense of such reconstructions. Bats are considered good indicators of changes in climate and vegetative cover (Stebbing, 1988) and include many endangered species throughout the world (International Union for the Conservation of Nature and Natural Resources (IUCN), 2000) and in Switzerland (Duelli, 1994; Moretti *et al.*, 2003).

Palaeoecological studies on bats based on radiocarbon dating allow reconstruction of the postglacial history of species recolonization and link these patterns to environmental evolution (e.g. vegetation composition and climate changes, see Postawa, 2004) in a landscape context (e.g. Neolithic deforestation, historic wild fires). Thanks to new sedimentary studies (e.g. Dapples *et al.*,

¹Swiss Institute for Speleology and Karst studies, Switzerland

²Swiss Federal Research Institute WSL, Insubric Ecosystems Research Group, Switzerland

³Bat Protection Center Ticino (CPT), Switzerland

⁴Institute of Plant Sciences (IPS) and Oeschger Centre for Climate Change Research (OCCR), University of Bern, Switzerland

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Corresponding author:

Michel Blant, Swiss Institute for Speleology and Karst Studies,
Box 818, CH-2301 La Chaux-de-Fonds, Switzerland
Email: michel.blant@isska.ch

Table 1. Repartition, ecology and status of bats studied (after Meschede and Heller, 2000; Mitchell-Jones *et al.*, 1999)

Species	Repartition in Europe	Roost sites	Foraging habitat	Alimentation	IUCN status
<i>R. hipposideros</i>	W, C, S	Buildings, caves (S)	Deciduous woodland, mixed and riparian forests	Diptera, Lepidoptera, Neuroptera	Vulnerable
<i>M. bechsteinii</i>	W, C, (S)	Hollow trees	Deciduous woodland (mature beeches and oaks), natural forests	Lepidoptera, Diptera, Planipennia	Vulnerable
<i>M. blythii</i>	C, S, E	Buildings, caves	Semi-arid open habitats	Orthoptera	Least concern
<i>M. myotis</i>	W, C, E, S	Buildings, caves	Forests, pasture	Coleoptera	Near threatened
<i>M. brandtii</i>	N, C, (S-E)	Buildings	Woodland and water areas	Lepidoptera, Diptera	Least concern
<i>M. nattereri</i>	N, C, E, (S)	Hollow trees, buildings	Woodland and sheltered water areas	Diptera, Coleoptera, Opiliones, Araneae	Least concern
<i>M. mystacinus</i>	N, C, E, (S)	Buildings	Woodland, structured landscape, riparian vegetation	Diptera, Arachnida, Lepidoptera	Least concern
<i>M. daubentonii</i>	W, C, N, E, (S)	Hollow trees, bridges	Lakes, rivers, ponds beyond deciduous, mixed forests	Diptera, Lepidoptera, Hemiptera, Trichoptera, Ephemeroptera, Coleoptera	Least concern
<i>M. emarginatus</i>	C, S	Buildings, caves	Agricultural structured landscape, mixed beech forests	Diptera, Araneae	Vulnerable

N, W, C, S, E: Northern, Western, Central, Southern, Eastern Europe. In parentheses: repartition dispersed, only patches

2002; Heiri *et al.*, 2003b; Tinner *et al.*, 1999, 2005) chronologically reliable palaeoclimatic and palaeoenvironmental data are abundant. A comparison between ancient environments and bat dynamics may contribute to a better understanding of future species responses to climatic, environmental and land-use changes (Intergovernmental Panel on Climate Change (IPCC), 2007; Seneviratne *et al.*, 2006).

Following an assessment of the composition and chronology of Holocene bat deposits found in Canalone Cave on Mt Generoso in southern Switzerland and its linkage to forest-dynamic patterns in the same region (Blant *et al.*, 2004, 2007), this research aims to enlarge the scale of observation to the ensemble of Holocene bats in the Swiss Alps by including samples of important collections from the Northern Swiss Alps. Such data have not been used previously in advanced chronological and palaeoecological analyses. In fact, most of the bone remains were stored in different places and only a small portion had been dated.

In this study we assess the extent to which Holocene bats can be applied as palaeoenvironmental indicators and which environmental factors (e.g. climate) can explain the occurrence of the species through time, in order to test the climate–vegetation relationship of Holocene bat composition in alpine context. At the same time we consider important information about the functional aspects of the forest succession during different times. We do this by reconstructing the presence of thermophilous taxa (i.e. preferring Atlanto-Mediterranean conditions, thus warm-demanding species) and psychrophilous taxa (i.e. preferring the colder climates of Boreo-Alpine conditions, thus cold-tolerant species). We then compare our data with independent palaeoenvironmental (i.e. pollen) and palaeoclimatic (i.e. chironomid-inferred temperatures) series.

Material and methods

Species selection

The bat species selected for this study were chosen because most of their ecological requirements are related to forests, which

allow the comparison of their population dynamic with the evolution of climate and vegetation during the Holocene. We also included some species that require open and semi-open habitats to assess their response to forest structures and successional stages. In addition, the species selected were relatively frequent in the fossil record and also currently present among the bat fauna of Switzerland (ecology of species see Table 1).

The most abundant thermophilous taxon selected was the Bechstein's bat (*Myotis bechsteinii*), a species that can be considered as a 'tracer of Quaternary warm periods' (Baagøe, 2001). Additional thermophilous species selected were the Lesser horseshoe bat (*Rhinolophus hipposideros*), the Lesser mouse-eared bat (*Myotis blythii*), and the Greater mouse-eared bat (*M. myotis*), the latter being considered a meso-thermophilous species. Among the psychrophilous species, the most important taxa was the Brandt's bat (*Myotis brandtii*), associated with the Natterer's bat (*Myotis nattereri*). Two other psychrophilous species, the Daubenton's bat (*Myotis daubentonii*) and the Whiskered bat (*Myotis mystacinus*), were also dated because of their deep stratigraphic location in our samplings, thus suggesting an interesting old age for these remains.

Study sites

The difficulty of studying bats for palaeoenvironmental reconstruction is mainly the lack of vertical stratification in bat remains, which are mainly spread on the cave floor. It was thus necessary to analyse and date enough material from different regions, similar to the methods applied in anthracology (e.g. Carcaillet, 1997; Carcaillet and Thinon, 1996).

The material used for dating comes from various sampling campaigns carried out in four caves located in the prealpine Swiss region on both southern (Canalone cave, Mt Generoso, Ticino canton, 1465 m a.s.l.) and northern slope of the Alps (Bettenhöhle and Schratthöhle caves, Mts Melchsee-Frutt, Obwald canton, 1719 m a.s.l.; D7.1 cave, Mt Sieben Hengste, Berne canton, 1746

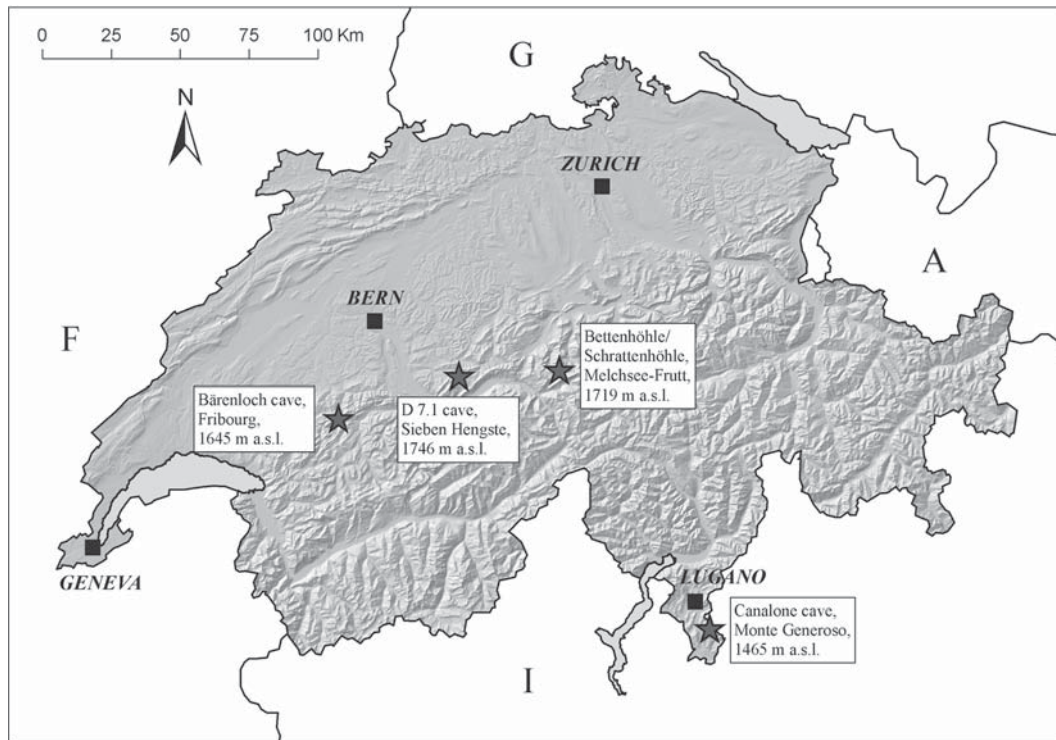


Figure 1. Map showing the geographical location of the studied caves (stars) with Holocene bat remains

Table 2. Environmental characterisation of the sites (temperature, precipitations and snow cover after the Swiss Climate Atlas)

Cave	Bärenloch cave	D 7.1 cave	Bettenhöhle/ Schrattenhöhle	Canalone cave
Altitude	1645 m a.s.l.	1746 m a.s.l.	1719 m a.s.l.	1465 m a.s.l.
Climate	Oceanic-alpine	Oceanic-alpine	Oceanic-alpine	Insubric-alpine
Year mean temperature	2–3°C	1–2°C	0–1°C	4–5°C
Year mean precipitation	2000 mm	2000 mm	1800 mm	2000 mm
Snow cover in March	70–100 cm	100–150 cm	150–200 cm	70–100 cm
Vegetation duration	100–120 days	80–100 days	55–80 days	135–150 days
Vegetation zone	Subalpine	Subalpine+	Subalpine	Mountain
Typical forest composition of the level	Silver fir-beech wood, maple wood	Spruce and silver fir woods	Spruce and silver fir woods	Beech-fir wood
Landscape on site	Stone fall	Karren field, lapié	Karren field, lapié	Grassland

m a.s.l.; Bärenloch cave, Mt Spitzflue, Fribourg canton, 1645 m a.s.l.) (Figure 1). More environmental information is provided in Table 2. Most material has been recently collected (2000 to 2005 for Canalone and Bärenloch caves) while older samples (> 10 years) are also used (1983 to 1998 for Bettenhöhle, Schrattenhöhle and D7.1 caves). Samples were conserved at the Archaeozoological Laboratory of the Museum of Archaeology and the University of Neuchâtel (Switzerland).

Data processing

The sampling selection was carried out by a randomized collection of material in the different study sites, with samples being selected in different sections and depths in each cave. The bat remains identified and analysed were only skulls or cranial fragments partly

including dental lines (upper premolars and molars). Species identification was based on cranial and teeth form (i.e. dental length, cuspids number or dental surface) following Menu and Popelard (1987) and Blant *et al.* (2008).

In order to obtain the best possible number of dating replications, we selected a total of 45 samples in four consecutive series, chosen in order to maximize the chronologic interval for each species considered. The results from each series determined the choice of individuals to be dated in the following step. Radiocarbon dating was carried out at the Institute of Physics of Particles of the Swiss Federal Institute of Technology (ETH) in Zurich by means of Accelerated Mass Spectrometry (AMS). The calibration (2σ , 95% interval) was performed with the CalibETH (Niklaus *et al.*, 1992, ETH-26518 to ETH-31333) or OxCal v3.10 programs (Ramsey, 2001, ETH-32810 to ETH-34036).

Palaeovegetation and palaeoclimate

In our study we used palaeobotanical data from sedimentary archives such as lakes and mires from the different Swiss regions according to Burga and Perret (1998). For the southern Alps, we considered the work by Tinner *et al.* (1999) from Lago di Origgio (416 m a.s.l.) near Lugano. For the northern Alps, we referred to the studies by Wegmüller and Lotter (1990) on the vegetation shifts in the mountains (Aegelsee, 995 m a.s.l.) and subalpine regions. Additional complementary data were found in Sidler (1992) for a Obbürgen-Merlialp transect in the northeastern pre-alpine regions, in Heiri *et al.* (2003b) and Wick *et al.* (2003) for Hinterburgsee (1515 m a.s.l.) and Sägistalsee (1935 m a.s.l.) in the northern regions, and in Dapples *et al.* (2002) and Welten (1982) for Schwarzsee (1046 m a.s.l.), and in Lenk (1885 m a.s.l.) for the northwestern regions. Data from the Swiss Plateau were found in Lotter (1999) for Soppensee (596 m a.s.l.) and in Ammann (1989) for Lobsigensee (514 m a.s.l.), while the Swiss Jura reported by Wegmüller (1966) from the Coinsins peat bog. Pollen assemblage zones (PAZ) and published diagrams allow a synthetic reconstruction of plant succession on the southern and northern Alps.

We assume that the hibernating sites used by bats, e.g. caves situated in the mountain and subalpine belts, had summer bat populations reproducing in the nearby lower altitudes, i.e. from the hill to the lower mountain belt.

As a proxy for Holocene temperatures, we use summer air temperature (i.e. July) reconstructed on the basis of past Chironomidae assemblages from the subalpine lake Hinterburgsee (1515 m a.s.l.) in the Bernese Oberland by Heiri *et al.* (2003a). It is the only Holocene quantitative temperature reconstruction for the Alps, successfully checked with other proxies of summer temperature change, e.g. treeline oscillations. This temperature reconstruction has been used by Heiri *et al.* (2006) to develop dynamic vegetation models, which have been successfully validated by independent palaeovegetational reconstructions from other regions in the Alps. The chironomid-inferred temperature curve (Heiri *et al.*, 2003a) is further well correlated with Holocene climatic oscillations on the Swiss Plateau and in the Austrian, Italian, and Swiss Alps (Haas *et al.*, 1998), suggesting that July air temperature is an outstanding proxy for the course of Holocene palaeoclimate in Central Europe. We assume that this reconstruction ideally represents the climatic variations undergone by bat populations during the main activity season (spring and summer), with extreme cold winter temperatures that do not affect these animals since bats overwinter by hibernating. On the other hand, the summer climatic variations can be considered a reliable proxy of the overall favourable ecological and trophic conditions for insectivores such as bats.

Results

Radiocarbon dates (Table 3) are reported in Figure 2 in relation to Holocene periods (chronozones) and archaeological ages for Central Europe. Only one sample (ETH-31323), caused problems resulting in a large age confidence interval, probably due to its very low weight (only front part of the crane).

Fourteen dates obtained on *Myotis bechsteinii* cover the interval between 8205–7957 cal. BP and 1523–1332 cal. BP, thus comprising a period from the end of the Boreal to the sub-Atlantic

(Figure 2). The oldest were collected in the Canalone cave in the Ticino Prealps, while the most recent were collected in the Sieben Hengste range in the Bernese Prealps. One radiocarbon sample of *Rhinolophus hipposideros* collected in the Canalone cave resulted in an age of 8079–7884 cal. BP, thus falling into the onset of the Atlantic (Figure 2).

Four dates from *Myotis blythii* samples fall into the interval 10690–10290 cal. BP and 6410–6180 cal. BP, covering thus the periods from the Preboreal to the recent Atlantic. All samples were collected in the Canalone cave. Two dates on *Myotis myotis*, both collected in the Canalone cave, provided ages of 2150–1890 cal. BP and 150–20 cal. BP, i.e. they fall into the sub-Atlantic period (Figure 2). Thirteen dates of *Myotis brandtii* samples cover the intervals 8218–7970 cal. BP and 1520–1290 cal. BP, thus comprising a period from the end of the Boreal to the sub-Atlantic. The oldest samples were collected in the Canalone cave, while the most recent come from Bettenhöhle in the Melchsee-Frutt massif in the Obwald Prealps (Figure 2).

Eight datings of *Myotis nattereri* cover the intervals between 9430–9020 cal. BP and 790–660 cal. BP, i.e. they extend from the Boreal to the sub-Atlantic period (Figure 2). The oldest were collected in the Canalone cave and the most recent in the Bettenhöhle. The only *Myotis mystacinus* sample was dated at 2120–1860 cal. BP, i.e. into the sub-Atlantic, and came from the Bettenhöhle. Two samples of *Myotis daubentonii* fell into the intervals 8367–8108 cal. BP and 3210–2920 cal. BP, i.e. in the Atlantic and sub-Boreal periods (Figure 2). The oldest was sampled in the Canalone cave, while the most recent came from the Bettenhöhle.

Discussion

Bat history

Our findings indicate the presence of bats at Mt Generoso in the southern Swiss Alps during the early Holocene, i.e. at least since 10 500 cal. BP. In the northern Alps, our results show a lag of *c.* 3000 years, with the oldest aged at approximately 7400 cal. BP. This suggests that the southern pre-alpine caves could have been already occupied by some species during the Lateglacial, i.e. before 11 500 cal. BP. The occurrence of bats (e.g. *Myotis nattereri*) north of the Alps at this time (Topál, 2001b) confirms this hypothesis. In the southern Carpathian Mountains, colonization by bats seems to start only during the Boreal period (Carbonnel *et al.*, 1999), i.e. shortly after our earlier dating in the southern Alps, but significantly after the end of the Lateglacial. The high altitude of our caves north of the Alps (1600–1800 m a.s.l.) might have been the limiting factor for an occupation during that period, possibly because of the high accumulation of snow or ice during most of the year. The quasi overlap of the oldest dates in the samples at the end of the older Atlantic period seems to indicate that the colonization of these three caves north of the Alps had occurred simultaneously. Our dates are 1000 years older than the oldest recorded by Postawa (2004) in southern Poland. The difference in timing of bat population buildups north and south of the Alps is comparable with that observed for vegetation. For instance a similar time-lag of 1000–3000 years occurred between the establishment of mixed oak forests south and north of the Alps (e.g. Finsinger *et al.*, 2006; Tinner *et al.*, 2005; Vescovi *et al.*, 2007; Figure 3).

Table 3. Dating results: species, locality, year of collection, radiocarbon age BP, calibrated age BC/AD, probability of calibration interval and age BP calibrated

Lab ID	Species	Year	Locality	Age BP	Calibration	Probability	Age BP cal.
ETH-26518	<i>Myotis bechsteinii</i>	1995	Canalone, Monte Generoso	3865±60	2467–2172 BC	(96.2 %)	4417–4122
ETH-26519	<i>Myotis bechsteinii</i>	2000	Canalone, Monte Generoso	5325±60	4261–4031 BC	(86.9 %)	6211–5981
ETH-26520	<i>Rhinolophus hipposideros</i>	2002	Canalone, Monte Generoso	7180±65	6129–5934 BC	(87.5 %)	8079–7884
ETH-27419	<i>Myotis bechsteinii</i>	2001	Canalone, Monte Generoso	5765±60	4729–4491 BC	(92.2 %)	6679–6441
ETH-27420	<i>Myotis bechsteinii</i>	2002	Canalone, Monte Generoso	7345±65	6255–6007 BC	(92.4 %)	8205–7957
ETH-27421	<i>Myotis daubentonii</i>	2001	Canalone, Monte Generoso	7455±70	6417–6158 BC	(97.1 %)	8367–8108
ETH-31322	<i>Myotis brandtii</i>	2002	Canalone, Monte Generoso	7320±75	6268–6020 BC	(89.0 %)	8218–7970
ETH-31323	<i>Myotis brandtii</i>	2002	Canalone, Monte Generoso	5130±115	4168–3693 BC	(94.4 %)	6118–5643
ETH-31324	<i>Myotis brandtii</i>	2002	Canalone, Monte Generoso	6870±70	5845–5632 BC	(94.4 %)	7795–7582
ETH-31325	<i>Myotis brandtii</i>	2002	Canalone, Monte Generoso	5330±60	4258–4037 BC	(84.9 %)	6208–5987
ETH-31326	<i>Myotis bechsteinii</i>	1988	Sieben Hengste/D7.I	1535±45	AD 427–618	(100.0 %)	1523–1332
ETH-31327	<i>Myotis bechsteinii</i>	1989	Sieben Hengste/D7.I	5705±60	4694–4446 BC	(94.2 %)	6644–6396
ETH-31328	<i>Myotis brandtii</i>	1989	Sieben Hengste/D7.I	1595±50	AD 381–583	(95.3 %)	1569–1367
ETH-31329	<i>Myotis brandtii</i>	1989	Sieben Hengste/D7.I	4485±60	3360–3014 BC	(95.8 %)	5310–4964
ETH-31330	<i>Myotis bechsteinii</i>	2005	Bärenloch am Spitzflue	4460±60	3347–3008 BC	(89.7 %)	5297–4958
ETH-31331	<i>Myotis bechsteinii</i>	2005	Bärenloch am Spitzflue	4730±55	3639–3492 BC	(62.8 %)	5589–5442
ETH-31332	<i>Myotis brandtii</i>	2005	Bärenloch am Spitzflue	6410±70	5483–5259 BC	(99.0 %)	7433–7209
ETH-31333	<i>Myotis brandtii</i>	2005	Bärenloch am Spitzflue	4840±65	3715–3506 BC	(89.8 %)	5665–5456
ETH-32810	<i>Myotis bechsteinii</i>	2002	Canalone, Monte Generoso	7135±60	6110–5880 BC	(93.0 %)	8060–7830
ETH-32811	<i>Myotis bechsteinii</i>	2002	Canalone, Monte Generoso	3550±75	2050–1680 BC	(91.8 %)	4000–3630
ETH-32812	<i>Myotis brandtii</i>	2002	Canalone, Monte Generoso	7210±65	6230–5980 BC	(95.4 %)	8180–7930
ETH-32813	<i>Myotis nattereri</i>	2002	Canalone, Monte Generoso	7450±65	6450–6210 BC	(95.4 %)	8400–8160
ETH-32814	<i>Myotis nattereri</i>	2001	Canalone, Monte Generoso	8245±75	7480–7070 BC	(95.4 %)	9430–9020
ETH-32815	<i>Myotis nattereri</i>	2002	Canalone, Monte Generoso	4210±50	2820–2630 BC	(65.5 %)	4770–4580
ETH-32816	<i>Myotis blythii</i>	2001	Canalone, Monte Generoso	9315±65	8740–8340 BC	(95.4 %)	10 690–0290
ETH-32817	<i>Myotis blythii</i>	2002	Canalone, Monte Generoso	9155±70	8560–8250 BC	(95.4 %)	10 510–10 200
ETH-33095	<i>Myotis bechsteinii</i>	1996	Bettenhöhle	5470±60	4460–4220 BC	(92.7 %)	6410–6170
ETH-33096	<i>Myotis bechsteinii</i>	1998	Bettenhöhle	6310±60	5390–5200 BC	(81.8 %)	7340–7150
ETH-33097	<i>Myotis bechsteinii</i>	1997	Bettenhöhle	5915±50	4940–4680 BC	(95.4 %)	6890–6630
ETH-33098	<i>Myotis bechsteinii</i>	1995	Bettenhöhle	5725±60	4720–4450 BC	(95.4 %)	6670–6400
ETH-33099	<i>Myotis brandtii</i>	1988	Schrattenhöhle	1480±50	AD 430–660	(95.4 %)	1520–1290
ETH-33100	<i>Myotis brandtii</i>	1996	Bettenhöhle	1955±45	60 BC–AD 140	(95.4 %)	2010–1810
ETH-33101	<i>Myotis brandtii</i>	1996	Bettenhöhle	2140±50	360–40 BC	(95.4 %)	2310–1990
ETH-33102	<i>Myotis brandtii</i>	1983	Bettenhöhle	1880±50	AD 20–250	(95.4 %)	1930–1700
ETH-33103	<i>Myotis nattereri</i>	1983	Bettenhöhle	775±45	AD 1160–1290	(95.4 %)	790–660
ETH-33104	<i>Myotis nattereri</i>	1998	Bettenhöhle	1525±50	AD 420–640	(95.4 %)	1530–1310
ETH-33105	<i>Myotis daubentonii</i>	1983	Bettenhöhle	2900±50	1260–970 BC	(92.2 %)	3210–2920
ETH-33106	<i>Myotis mystacinus</i>	1983	Bettenhöhle	2010±50	170 BC–AD 90	(95.4 %)	2120–1860
ETH-34030	<i>Myotis blythii</i>	2001	Canalone, Monte Generoso	7870±70	7040–6590 BC	(95.4 %)	8990–8540
ETH-34031	<i>Myotis myotis</i>	2002	Canalone, Monte Generoso	40±45	AD 1800–1930	(66.9 %)	150–20
ETH-34032	<i>Myotis blythii</i>	2002	Canalone, Monte Generoso	5495±60	4460–4230 BC	(95.4 %)	6410–6180
ETH-34033	<i>Myotis myotis</i>	2002	Canalone, Monte Generoso	2060±50	200 BC–AD 60	(95.4 %)	2150–1890
ETH-34034	<i>Myotis nattereri</i>	2005	Bärenloch am Spitzflue	1135±50	AD 770–1020	(95.4 %)	1180–930
ETH-34035	<i>Myotis nattereri</i>	2005	Bärenloch am Spitzflue	5010±60	3960–3690 BC	(93.2 %)	5910–5640
ETH-34036	<i>Myotis nattereri</i>	1989	Sieben Hengste/D7.I	6070±60	5210–4830 BC	(95.4 %)	7160–6780

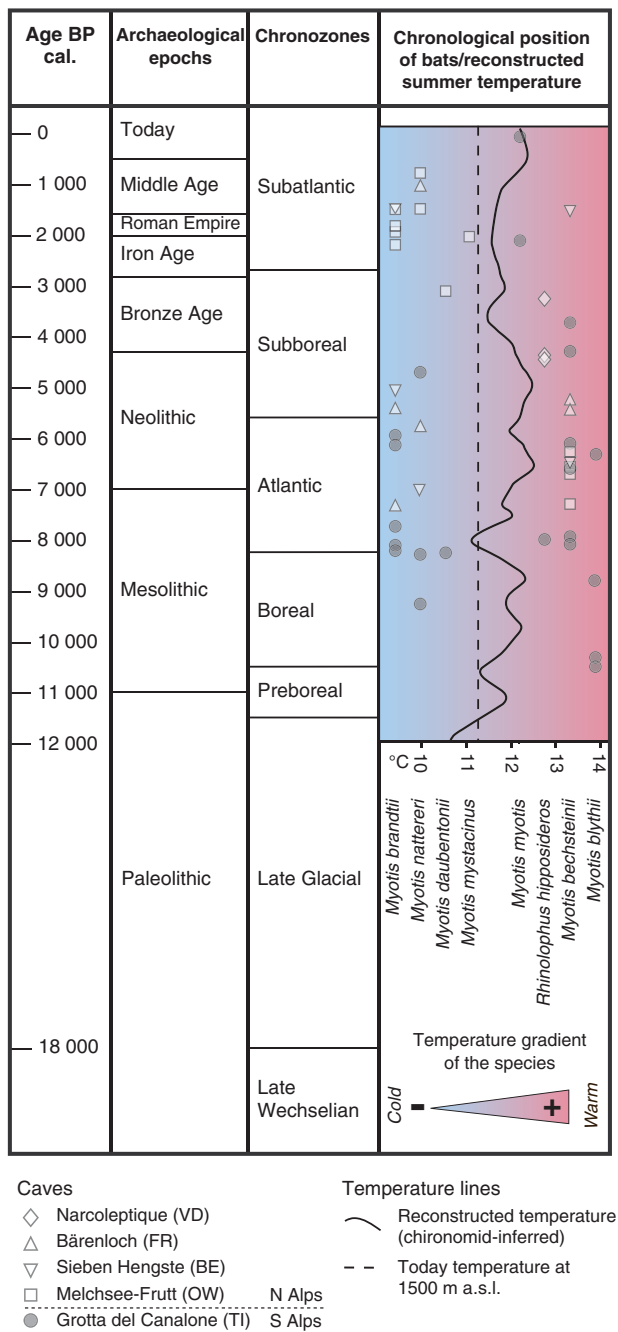


Figure 2. Archaeological epochs, Holocene periods (chronozones after Firbas, 1949, 1954 and Lang, 1994), chronological position of bat findings, and the quantitative chironomid-inferred Alpine Holocene summer temperature reconstruction according to Heiri *et al.* (2003a). Filled symbols in the right-hand side of the figure refer to the bat records from the southern Alps; blank symbols to those from the northern Alps. Details of their provenance are given in the legend

The linkage between bat and vegetation changes

The major number of samples of *Myotis bechsteinii*, characteristic species of deciduous thermophilous forests (Baagøe, 2001; Meschede and Heller, 2000), provided early Atlantic to sub-Boreal ages (8200–2800 cal. BP). In the lowlands of the southern Alps (< 1000 m a.s.l.), thermophilous forests, dominated by *Abies alba*, *Tilia* sp., *Quercus* sp., *Fraxinus excelsior* and *Ulmus* sp. (Figure 3) occurred after c. 9200 cal BP. This particular thermophilous forest

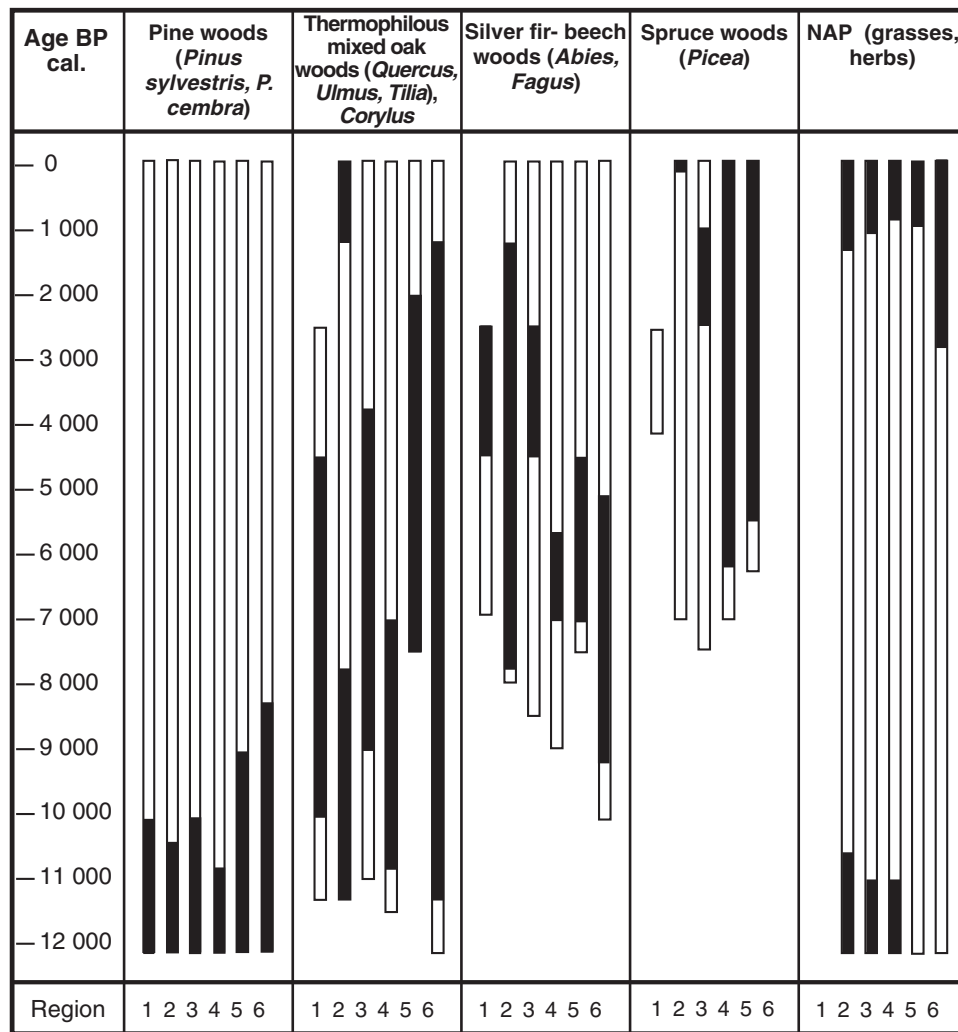
type has no modern analogue (Tinner *et al.*, 1999), and in the lowlands of the southern Alps and Prealps it became extinct c. 5000–4000 years ago (Tinner and Ammann, 2005) mainly as a result of anthropogenic fire and land use. These forests were replaced by fire-tolerant and rather open *Quercus* and *Alnus* woods until the expansion of *Castanea sativa* c. 2000 years ago (Tinner *et al.*, 1999).

On the Swiss Plateau north of the Alps, mixed-oak forests were gradually replaced by *Abies alba* and *Fagus sylvatica* at c. 8000–6000 cal. BP. These two species are among the most important in today's forests (Tinner and Lotter, 2001, 2006). The lowland vegetation in the northern Prealps was similar to that on the Swiss Plateau, whereas more psychrophilous trees, such as *Pinus sylvestris*, *Betula pendula*, *Pinus cembra* and, after c. 5000 cal. BP also *Picea abies*, were more important at higher altitudes (Dapples *et al.*, 2002; Heiri *et al.*, 2003b; Sidler, 1992; Wegmüller and Lotter, 1990). Treeless openlands were established for agricultural purposes during past millennia and reached the current situation during or after the Iron Age (i.e. after 2800 cal. BP).

Our results suggest a decline of *Myotis bechsteinii* populations that started c. 5000 cal. BP, in the middle of the Neolithic period. Only one date of this species fell in the sub-Atlantic period starting at 2800 cal. BP, when the occurrence of cultivated openlands (e.g. Poaceae, NAP) was comparable with today's situation on the northern and southern slope of the Swiss Alps (Figure 3) (Lotter, 1999; Tinner *et al.*, 1999; Wegmüller and Lotter, 1990). The shift from mixed oak to beech forests might have induced a slow habitat deterioration for this species, which has been worsened by forest clearing and cut-and-burn practices (Tinner and Lotter, 2006). *Myotis bechsteinii*, described as 'primeval forest bat', depends on stable habitat conditions (Schlapp, 1990) and can be negatively influenced by changes in the forest structure. As this species is climatically restricted to the lowland (Meschede and Heller, 2000), mountain forests were not suitable as alternative habitat for the loss of the forests in the plains. To this regard our results contrast with the study by Postawa (2004) in Poland, where *M. bechsteinii* dominated in beech forests during the sub-Boreal. However, our results confirm the decline of the *M. bechsteinii*'s population in the sub-Atlantic, when deciduous forests became substantially disrupted (Wołoszyn, 1987). Observations by Postawa (2004) indicate that epidemic disease may also reduce *M. bechsteinii*. *Myotis emarginatus*, another species of lowland deciduous forests (Topál, 2001a), might have undergone a similar decline as *M. bechsteinii* in our results. Indeed, Meschede and Heller (2000) noted that the species was more common before the onset of large-scale deforestations, e.g. in Bavaria in southern Germany. The only date available for this species in Switzerland (Morel and Trüssel, 1997) goes back to the beginning of the Middle-Ages.

The preference of high-quality well-structured habitats by *M. bechsteinii* and *M. emarginatus* to capture prey on foliage (glaning) makes both species sensitive to modifications of forest structure and composition. Bauer (1987) noted that after the introduction of agriculture (from Neolithic onwards), *M. bechsteinii* declined while *M. myotis* increased. The latter species captures ground-dwelling prey on forest soils with poor vegetation, thus fire impact and conifer plantation (both usually resulting in impoverished forest habitats in our area) may explain this shift in past bat communities.

Rhinolophus hipposideros occurred at c. 8000 cal. BP during the older Atlantic period in the southern Alps, i.e. in the same



Pollen

— dominating or sub-dominating

▭ present

Region, local site name, reference

1 Jura, Bog of Coinsins (Wegmüller 1966)

2 Plateau, Soppensee (Lotter 1999)

3 N-E Prealps, Obbürgen-Merlialp (Sidler 1992)

4 N-Centre Prealps, Hinterburgsee (Heiri *et al.* 2003b)

5 NW Prealps, Wallbach/Lenk (Welten 1982), Schwarzsee (Dapples *et al.* 2002)

6 S Prealps, Lago di Origlio (Tinner *et al.* 1999)

Figure 3. Schematic duration of predominant vegetation types north and south of the Alps

forest environment as *M. bechsteinii*. This species is assumed to have colonized Central Europe during the early Holocene (Horáček, 1984). Three other datings of *R. hipposideros* from the cave of Narcoleptique 1265 m in the Swiss Jura Mountains fall into the interval 4800–3000 cal. BP in the sub-Boreal (Oppliger, 2007). In this area mixed beech forest had already replaced the mixed oak-forest at lower altitudes (Figure 3). At that time the forests of the upper Swiss Plateau and of the northern Alps were dominated by silver fir (*Abies alba*), partly together with spruce (*Picea abies*) and some beech (Lotter, 1999; Wehrli *et al.*, 2007). The woods of the Jura Mountains are more favourable for *R. hipposideros*, which prefers thermophilous broadleaved forests, although hunting was also important in other more mesophilous and mixed vegetation types (Bontadina *et al.*, 2002, 2006).

Myotis blythii appeared in the southern Alps during the Preboreal chronozone (11600–9800 cal. BP), mainly occupying open thermophilous but markedly continental forests with *Pinus sylvestris*, *Quercus*, *Corylus*, *Ulmus*, *Betula*, *Fraxinus excelsior* and *Tilia* as dominant species (Tinner *et al.*, 1999) (Figure 3). Its presence continued during the Boreal and Atlantic periods (9800–5000 cal. BP), when forests became closer and co-dominated by *Abies alba*. Two *Myotis myotis* samples had late-Holocene ages, when vegetation was characterized by *Quercus* and *Castanea sativa* forests and openlands (Figure 3), as it is still today (Tinner *et al.*, 1999). *Myotis blythii*, which is essentially a Mediterranean species, was not found in sites north of the Alps, whereas at present it occurs in mixed colonies with *M. myotis* in many locations of the central and eastern Swiss Alps (Valais, Grisons, Saint-Gall,

Arletta *et al.*, 1994). *Myotis blythii*, a species highly specialized in Orthoptera predation in well exposed grasslands (Arletta, 1995a, 1999; Güttinger, 1998), was probably able to expand during the onset of the Holocene, taking advantage of the open structure of the heliophilous (light demanding) oak-pine forests that occurred south of the Alps. During this period the species could have migrated from Asia to southern Europe and Iberian Peninsula (Sevilla, 1988). As expected, our results showed that *M. blythii* preceded the forest bats (such as *M. bechsteini*, *M. brandtii*, *M. nattereri*) by more than 1200 years. This could raise new questions about the suitability and functionality of the pinewood and thermophilous forests for the more restricted or more demanding mature forest bat species.

The dates of *Myotis brandtii* cover a long time interval, i.e. from the old Atlantic 8200 cal. BP to the middle of the sub-Atlantic approximately 1500 cal. BP. The species occurred particularly during two periods, the first extending from the Atlantic to the beginning of the sub-Boreal (8200–5000 cal. BP), and the second falling into the sub-Atlantic (2800–1500 cal. BP) period. The temporal occurrence of this boreal mountain species is similar to that of *M. bechsteini*, with its presence coinciding with the expansion of *Abies alba* and *Fagus sylvatica* into the mixed deciduous continental forests (Dapples *et al.*, 2002; Heiri *et al.*, 2003b; Sidler, 1992; Tinner *et al.*, 1999; Wegmüller and Lotter, 1990). In the southern Alps this species was well represented in the earlier Atlantic, in Canalone cave (Blant *et al.*, 2004), but it disappeared during the sub-Boreal together with the other psychrophilous species (Figure 2). Currently this boreal species (Strelkov, 1983) occurs in the cooler mountain belt (Meschede and Heller 2000; Zingg, 1984), where coniferous wood is abundant. Increasing disturbance by fire during the Bronze and Iron Ages 4200–2000 cal. BP (Tinner *et al.*, 1999) may partly explain this long-term decline in the southern Alps, where wildfires were more frequent than in the north (Tinner *et al.*, 2005) and where they contributed to the decline of fire-sensitive mixed, partly coniferous forests in the colline and mountain belts. Postawa (2004) suggest that *M. brandtii* moved from Alpine and forest locations to lower locations, and *M. mystacinus* took its place.

The dates obtained for *Myotis nattereri* cover a period spanning from the Boreal 9800–8200 cal. BP to the sub-Atlantic (after 2800 cal. BP). This species was thus relatively frequent in the southern Alps when *Pinus sylvestris* and *Betula* forests were gradually replaced by thermophilous mixed-oak (*Quercus*) and hazel (*Corylus avellana*) woods (e.g. Tinner *et al.*, 1999; Figure 3). The oldest date from the northern Alps corresponds to the early Neolithic onset (c. 7500 cal. BP), when *Abies alba* and then *Fagus sylvatica* started to co-dominate in the upper mountain and partly in the lower subalpine belts (i.e. c. 800–1600 m a.s.l.) (Dapples *et al.*, 2002; Heiri *et al.*, 2003b; Sidler, 1992; Tinner and Ammann, 2005; Wegmüller and Lotter, 1990). At that age thermophilous mixed-oak forests were still abundant in the lower mountain and colline belts north of the Alps (Ammann, 1989; Dapples *et al.*, 2002; Tinner and Ammann, 2005; Wegmüller and Lotter, 1990). In this region the occurrence of *M. nattereri* lasted until the historic period, but south of the Alps this species declined together with *M. brandtii* during the sub-Boreal. A coeval regression of *M. nattereri* is reported by Postawa (2004) in southern Poland. Today *M. nattereri* is still represented in mountain belt forests with high proportion of coniferous wood (Meschede and Heller, 2000).

Remains of *Myotis mystacinus* and *M. daubentonii* fall into the Atlantic and sub-Boreal chronozones. These two species occurred during the same Holocene time interval as *M. brandtii* and *M. nattereri*. *Myotis mystacinus* is often well represented in Holocene records (Blättler *et al.*, 1995; Magnin, 1991; Morel, 1989). This species, which occurs in open environments in southeastern Europe, colonized the forests in Central Europe and Ural, overlapping the habitat of *M. brandtii* (Strelkov, 1983). *Myotis daubentonii*, which is usually poorly sampled in cave remains except in the Polish uplands with high water availability (Postawa, 2004; Roer and Schober, 2001), seems to be more abundant during humid and cool periods, whereas during warmer ones it is less abundant (Postawa, 2004). This species occurs in lowland and mountain belt forests (Meschede and Heller, 2000), but always in proximity of water bodies for chironomid hunting. However, more datings of both species are needed to consider their importance as environmental indicators.

Bat history and climatic change

Thermophilous species such as *Myotis bechsteini* mainly occurred during the climatic optimum in Central Europe spanning from c. 10 000 to 4000 cal. BP, i.e. Boreal to early sub-Boreal period (Figure 2). Their high proportion during this period suggests that the species were advantaged by optimal environmental conditions, supporting the hypothesis stressed by different authors (e.g. Bauer and Walter, 1977; Kowalski *et al.*, 1963; Liegl, 1987; Morel, 1989; Rupp, 1991; Schaefer, 1973; Wołoszyn, 1970, 1987) regarding their abundance in fossil Holocene records. Our findings clearly show that this optimum started long before the sub-Boreal period, as suggested by Bauer's datings from Katerloch (in Baagøe, 2001) and radiocarbon-dated assemblages in southern Poland (Postawa, 2004). The strong occurrence of *M. bechsteini* in our data during the warmest phases of the Holocene supports the hypothesis by Morel and Trüssel (1997) that thermophilous species were much more abundant in the past than today. In addition to warmer summer conditions, these species probably took advantage from forest expansion up to 2375–2500 m in the Alps during the Atlantic period, which is c. 300 m above today's average forest limit (Heiri *et al.*, 2006; Tinner and Theurillat, 2003). Moreover, a cluster of dates between 6800 and 6200 cal. BP for *M. bechsteini* corresponds to a long, particularly warm and dry climatic phase between two cold-humid phases in Central Europe CE-4, 7500–7100 cal. BP and CE-5, 6100–5650 cal. BP (Figure 1) (Haas *et al.*, 1998). Additional evidence of a positive response of thermophilous bats to warming during the Holocene climatic optimum comes from a sample of *Rhinolophus euryale* (typical Mediterranean species today) found in the Cave of Poteux in the Valais, Swiss Central Alps, that was dated at c. 4200 cal. BP (3870 ± 60 BP uncal. in Arletta, 1995b).

After the end of the Younger Dryas at 11 500 cal. BP, summer temperature gradually reached levels of c. +1°C if compared with today, which persisted between c. 10 000 and 4000 cal. BP (Heiri *et al.*, 2003a) despite some cooling periods. During the late Holocene a further cooling at 3500–3300 cal. BP (CE-6) definitively reduced summer temperatures (Heiri *et al.*, 2003a, 2006) (Figure 2). The psychrophilous species *Myotis brandtii* forms a cluster in the northern Prealps during the sub-Atlantic period 2300–1500 cal. BP, when summer temperatures declined gradually, reaching today's relatively cool levels in the Alps. Similar

increases were observed by Postawa (2004) for *M. daubentonii*, *P. auritus* and *M. dasycneme* during humid and cool periods as well as a dramatic decline of *M. nattereri* during climate cooling (and moistening) at 5500–5000 cal. BP. Overall, this suggests that bats responded sensitively to both, the general millennial course of Holocene temperatures as well as centennial-scale events. Although mean temperatures are influencing productivity in trophic chains, the relatively diverse diet of bat species (such as *R. hipposideros*, *M. bechsteinii*, *M. brandtii*, *M. nattereri*, *M. mystacinus* and *M. daubentonii*, Table 1) including well-represented taxa (i.e. Diptera, Lepidoptera) indicates that the availability of prey cannot be the only factor explaining the changing occurrence of bat species. Instead we conclude that changes in climate as well as forest composition and structure were the main trigger of bat community shifts during the Holocene.

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