

Hibernation phenologies and winter activities of four congeneric bat species hibernating simultaneously in an Eastern Alpine cave studied by phototrapping (Chiroptera: Vespertilionidae)

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Abstract. Using phototrapping, we compared hibernation phenologies and winter activities displayed by four *Myotis* species (*M. emarginatus*, *M. daubentonii*, *M. bechsteinii* and *M. nattereri*) hibernating in Hermann's Cave in the winter 2018/2019. These congeneric species were deemed to be comparable as they are similar in body mass and geographic distribution. The cave is located in the submontane zone of the Eastern Alps in Kirchberg am Wechsel, Lower Austria (47°37'N, 15°58'E, 670 m a. s. l.). From 1 September 2018 to 30 April 2019, we phototrapped a total of 67,183 emerging bats. These included, besides photos of other species, photos of 15,250 *Myotis nattereri*, 2,432 *M. bechsteinii*, 1,327 *M. emarginatus*, and 1,112 *M. daubentonii* individuals. Ambient temperature was measured hourly by a logger positioned at the cave entrance. Despite exposure to the same environmental conditions, the four species exhibited notable differences in their hibernation behaviour. The length of hibernation ranged from 19.5% of the year (*M. nattereri*) to 56% of the year (*M. emarginatus*), hibernation onset varied between 23 September (*M. emarginatus*, *M. daubentonii*) and 8 December (*M. nattereri*), and hibernation termination between 16 February (*M. nattereri*) and 15 April (*M. emarginatus*). Ambient temperature at the onset of hibernation ranged between 4.5 °C (*M. nattereri*) and >10 °C (in the other species). Ambient temperature at termination was higher than 10 °C only in *M. bechsteinii*. Winter activity expressed by post-arousal emergence flights during the species-specific hibernation period occurred in all months and was performed by all species. Over the total hibernation period (205 days), 179 post-arousal emergence flights were registered. The lowest number of flights was registered in January. The highest numbers in relation to the duration of stay in the cave were performed by *M. nattereri* and *M. emarginatus*, the lowest activity outside the cave was exhibited by *M. daubentonii* and *M. bechsteinii*. Diurnal activity was generally infrequent. Most flights occurred at $T_a > 0$ °C and numbers peaked at temperatures >6 °C. However, all species performed flights also at T_a between -4.5 and 0 °C. The temperature preference of *M. nattereri* differed distinctly from that of the other species. Most emergence flights of this species occurred at T_a between -5 °C and 6 °C. *Myotis emarginatus*, *M. daubentonii* and *M. bechsteinii* bats used ambient temperatures above 6 °C which is the low threshold for insect flights probably to hunt flying insects at the beginning and end of the hibernation periods. Flights performed by *M. emarginatus* around sunset seemed to have been used for light sampling. With the exceptions of *M. nattereri* and *M. emarginatus*, most emergence flights were carried out by only one individual of a particular species per bat day. On 8 October, four *M. emarginatus* emerged synchronously within one minute. No interspecific synchronous post-arousal flights were observed. Factors that could determine the hibernation behaviour such as the species origin, food and feeding strategies, circannual and circadian rhythms and ambient temperature are thoroughly discussed.

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Key words. Hibernation phenology, alpine cave, winter activity, phototrapping, *Myotis bechsteinii*, *Myotis daubentonii*, *Myotis emarginatus*, *Myotis nattereri*.

INTRODUCTION

Hibernation is most important for arthropodivorous temperate bats. It is associated with increased survival and the evolution of slow life (TURBILL et al. 2011) and considered to be an important factor explaining the exceptional longevity of bats (WILKINSON & SOUTH 2002, TURBILL et al. 2011, GEISER 2013). As hibernating bats are concealed from factors of extrinsic mortality and derive a benefit from retarded physiological deterioration, a long hibernation period is advantageous for individual survival. However, conserving sufficient energy to survive cold temperatures and food scarcity during winter and to reproduce successfully after hibernation is a big challenge (SPEAKMAN & RACEY 1989, HUMPHRIES et al. 2003). Most hibernating bat species rely on stored body fat accumulated in autumn (SPEAKMAN & ROWLAND 1999) and use torpor for energy saving. Torpor is a state of controlled reduction of body temperature and metabolic rate (GEISER 2004). However, using torpor has severe physiological costs caused by the build-up of metabolic wastes and dehydration stress through the inability to drink or urinate as well as by depressed heart- and breathing rate and depressed immune and protein synthesis (HUMPHRIES et al. 2003). To counteract these costs, bats interrupt torpor periodically by arousing to normal body temperature (DAAN 1973, HUMPHRIES et al. 2003, GEISER 2004, BOYLES et al. 2006, HOPE & JONES 2012). About 10% of hibernating bats perform emergence flights (DAAN 1973) during arousals and engage in outside cave activities, such as switching hibernacula, drinking, mating, and foraging to replenish their energy reserves (AVERY 1985). The organisation of hibernation is often governed by circannual and/or circadian rhythms that can be entrained by internal and external cues (Zeitgeber). An important Zeitgeber is the ambient temperature as it affects the food availability (KÖRTNER & GEISER 2000).

Only few studies comparing the phenologies of bat species hibernating under similar conditions (e. g. DAAN 1973, WERMUNDTSEN & SIIVONEN 2010, KUGELSCHAFTER & HENSLE 2017) exist and even less comparative information is available on the frequency and timing of winter activity during hibernation.

By analysing time-stamped photographs of four biologically comparable and reliably identified congeneric bat species emerging from a joint hibernaculum throughout a complete hibernation season, we are able to provide here exact information on (1) species-specific timing and duration of hibernation in relation to ambient temperature and (2) frequency and timing of post- arousal emergence flights in relation to ambient temperature. We discuss intrinsic and extrinsic factors that may explain the notable interspecific differences in phenology and in frequency and timing of post-arousal emergence flights.

This is the first study on hibernation behaviour conducted in a continental sub-mountain climate and results can thus be useful for comparison with a number of studies carried out in European maritime climates.

MATERIAL AND METHODS

Study site and date

Field work was carried out at Hermann's Cave in Kirchberg am Wechsel (47°37'N, 15°58'E), Lower Austria, from 1 September 2018 throughout 30 April 2019. Due to technical complications, phototrapping performed during the winter 2017/2018 was interrupted several times. The study period was thus limited

to one hibernal season, however, our dates concerning the onset and termination of hibernation of the four species studied can be considered as fairly representative as dates obtained in 2017/2018 and 2018/2019 differed by at most five days. Only *M. nattereri* arrived in the cave 15 days earlier in the autumn 2017 than in the following year.

The cave is located in a submontane mixed spruce forest at the foothills of the Eastern Alps. Mean annual precipitation and mean annual temperatures are 700–900 mm and 8.3 °C, respectively. The cave is a labyrinth-like system of mostly very narrow corridors 4.43 km in length and few large domes (maximum height 15 m). It has two known entrances, of which the upper one is accessible for bats through two openings (Fig. 1). The altitudes of the upper and lower entrances are 670 m and 627 m a. s. l., respectively (HARTMANN & HARTMANN 1997).

Corresponding to the complicated structure, Hermann's Cave is characterised by a wide range of microclimate conditions and seasonal changes in airflow. Intra-cave temperatures measured in the 1990s ranged between –1.9 °C and +24.8 °C (MRKOS 1993, TIESNER 1993, SKODA 1997). The large variety of microclimate offers many options for hibernating bats with different thermal preferences. This advantage and the availability of an open water source in the cave are essential prerequisites for successful hibernation and may be the reason for the high numbers of bat species recorded in this cave. In spite of being used as a show cave since 1845 (HARTMANN & HARTMANN 1997, MRKOS 1997), Hermann's Cave provides



Fig. 1. Position of phototraps containing cameras 1 and 2 at the two openings of Hermann's Cave used by bats.

Table 1. Dates of the onset and termination and duration of hibernation of four *Myotis* species; T_a measured on evenings of the onset and evenings of termination of the hibernation periods

| species | date of onset | T_a [°C] | date of termination | T_a [°C] | duration [days] |
|---------------------------|-------------------|------------|---------------------|------------|-----------------|
| <i>Myotis emarginatus</i> | 23 September 2018 | 14.0 | 15 April 2019 | 5.0 | 205 |
| <i>Myotis daubentonii</i> | 23 September 2018 | 14.0 | 9 March 2019 | 7.5 | 168 |
| <i>Myotis bechsteinii</i> | 20 October 2018 | 13.0 | 22 March 2019 | 10.5 | 154 |
| <i>Myotis nattereri</i> | 8 December 2018 | 4.5 | 16 February 2019 | 9.0 | 71 |

shelter for 17 bat species (BAAR et al. 1986 and own observations), which is the highest species number recorded in Austrian caves. It is legally protected under the EU Habitats Directive and closed for visitors between 1 November and 30 April.

Ambient temperature

Over the study period, the ambient temperature (T_a) was measured hourly with a data logger (Lascar EL-USB-2) at the upper entrance to the cave. All ambient temperatures mentioned refer to values recorded during twilight (one hour post sunset CET).

Light barriers and automated phototrapping

To record all bats emerging from the cave, two phototrapping units were set up at the two openings of the cave (Fig. 1). Each unit comprised a light barrier system (two subsequent rows of 16 beams each); a Tricorder 9008e (a data storage device that also triggers the camera system); fly-ins and fly-outs are registered separately based on logical interruptions of the light barriers, and two camera units (each comprised of two Panasonic-DMC-G5 cameras, two Metzblitz 58 flash and two flash detectors for fly-ins and fly-outs). The electric supply of the monitoring system was buffered by a large set of car batteries. The photographs were marked with date, hour, minute and second (CET). While the cameras at the lower opening worked throughout the study period, the cameras at the upper entrance (camera 2) did not function until 6 October 2018.

Definition of duration of hibernation and winter activity

The onset of hibernation is defined by the observation of the last emerging bat followed by 0 or <2 emergence flights at maximum, and termination of hibernation is defined by the last day on which less than two emergence flights after a period of hibernal inactivity have been observed. Winter activity outside the cave per bat day is defined by registration of post-arousal emergence flights during the species-specific hibernation period. The total hibernation period is the time span during which at least one of the studied species hibernated in Hermann's Cave. It ranges from 23 September 2018 to 15 April 2019.

Definition of a bat day and study species

A day is defined as the time between midnight and midnight, a bat day is defined as the time between midday and midday.

The studied species (*Myotis bechsteinii*, *M. daubentonii*, *M. emarginatus*, and *M. nattereri*) have basic biological traits in common which makes them comparable (DIETZ & KIEFER 2014). They are medium sized – average body mass in males between 6.2 g (*M. nattereri*) and 10 g (*M. bechsteinii*) – and share large parts of their distribution areas ranging from the Mediterranean to the Netherlands and Poland (*M.*

emarginatus), to southern England and southern Sweden (*M. bechsteinii*), to southern Scandinavia up to 60°N (*M. nattereri*), and to Scandinavia up to 66°N (*M. daubentonii*).

RESULTS

Number of photographs obtained

During the study period, we obtained a total of 67,183 photographs of bats identified to species emerging from the cave. The most frequently registered species was *Rhinolophus hipposideros* (46,483 photos), followed by *Myotis nattereri* (15,250 photos), *Myotis bechsteinii* (2,432 photos), *Myotis emarginatus* (1,237 photos), and *Myotis daubentonii* (1,112 photos). Further photos showed *Barbastella barbastellus* (394 photos) and *Myotis myotis* (139 photos), less than 100 photos were taken from *Rhinolophus ferrumequinum* and *Eptesicus serotinus*. Photographs of long-eared and whiskered bats could not be identified to species.

Length and timing of hibernation in relation to T_a

Length and timing of the hibernation period and ambient temperature at the onset and termination of hibernation varied notably among the four species studied (Table 1). The longest hibernation period was performed by *M. emarginatus* (Fig. 2). It lasted 29 weeks and two days (56.2% of

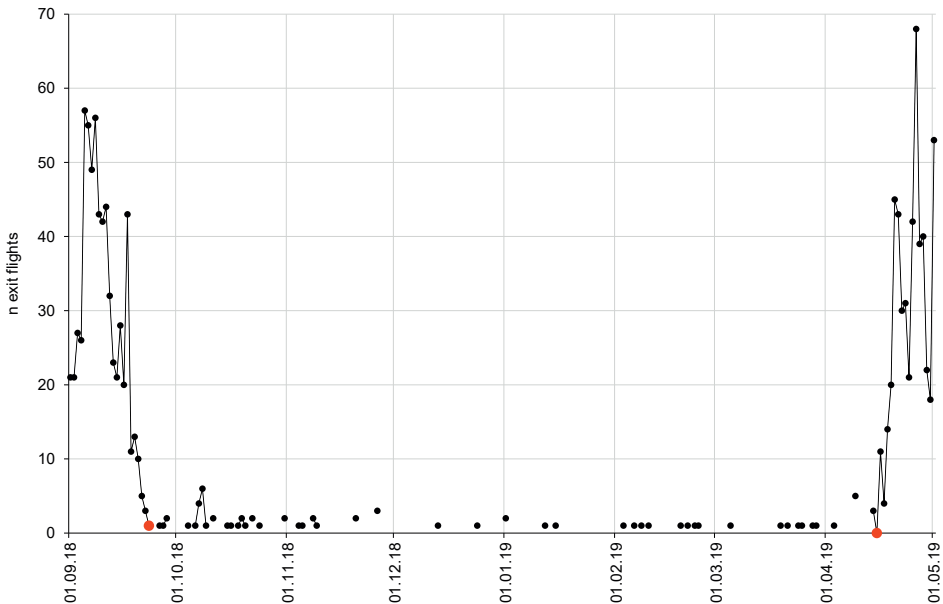


Fig. 2. Daily sums of emergence flights from Hermann's Cave per bat day performed by *Myotis emarginatus*. Red: dates of the onset and termination of hibernation. From 23 September to 6 October camera 2 did not function.

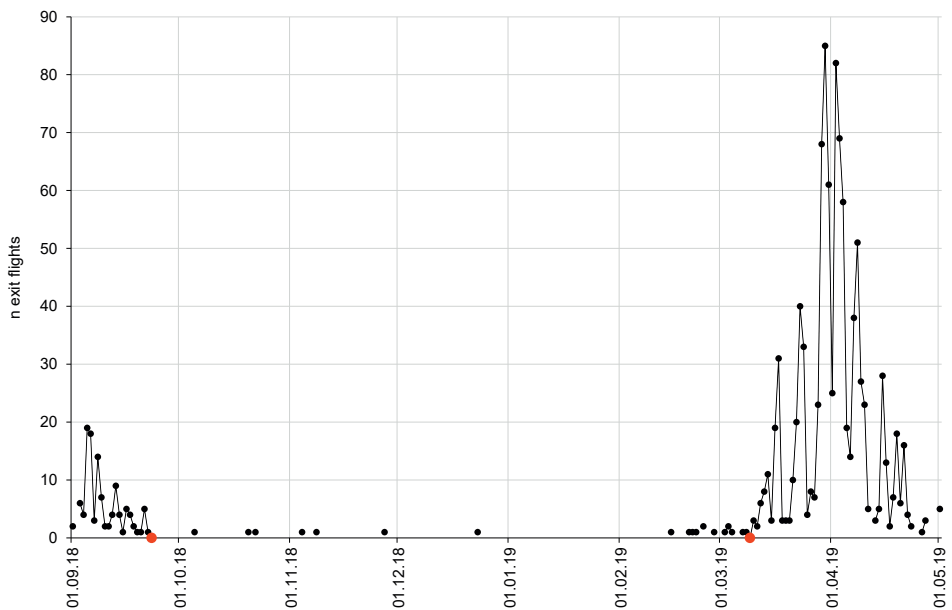


Fig. 3. Daily sums of emergence flights from Hermann’s Cave per bat day performed by *Myotis daubentonii*. Red: dates of the onset and termination of hibernation. From 23 September to 6 October camera 2 did not function.

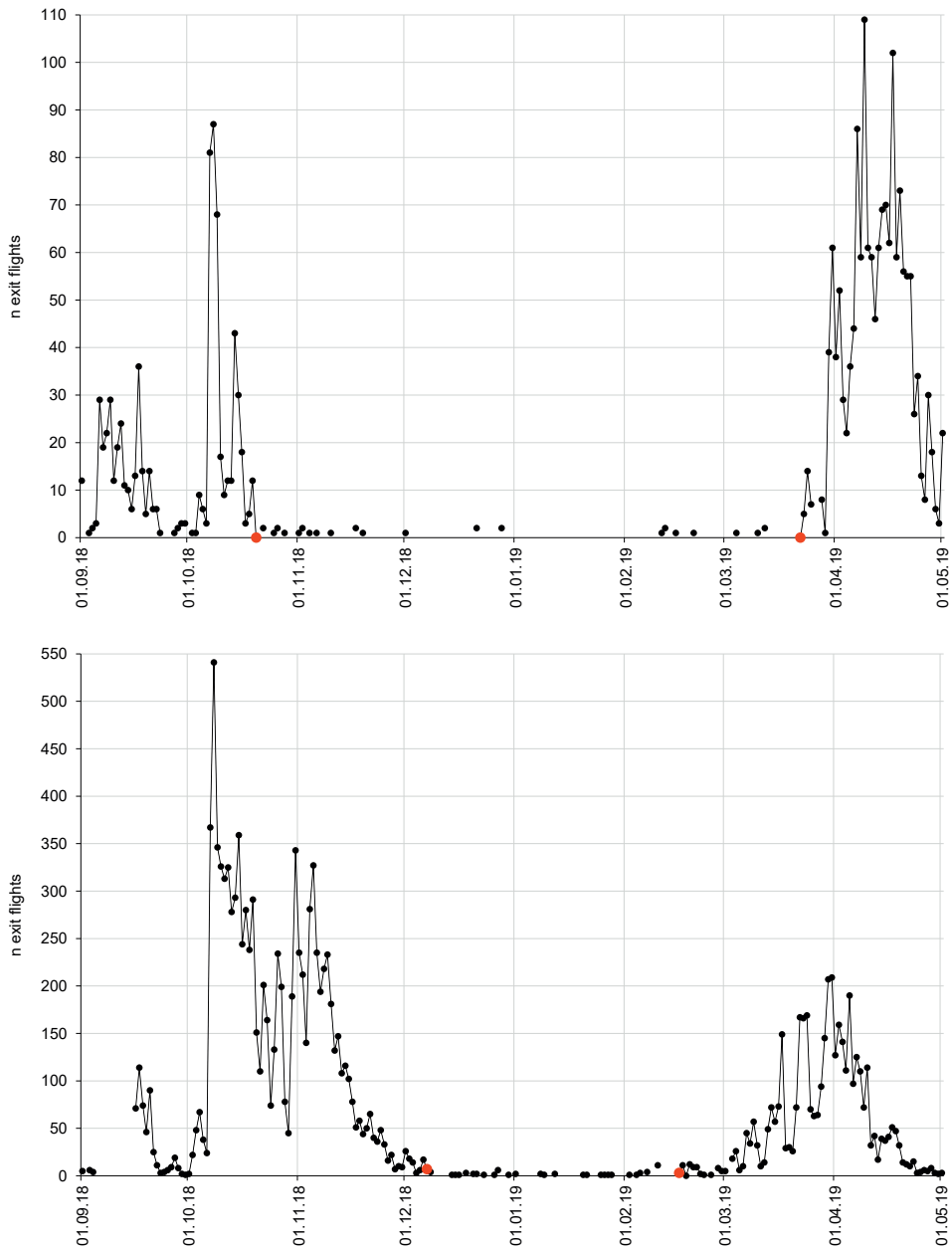
the year). *M. daubentonii* performed the second longest, lasting 24 weeks (46.0% of the year; Fig. 3); that of *M. bechsteinii* lasted 22 weeks (42.2% of the year; Fig. 4); that of *M. nattereri* bats was the shortest, lasting 10 weeks and one day (19.5% of the year; Fig. 5).

Similarly, the onset and termination of hibernation differed clearly: *M. emarginatus* and *M. daubentonii* started hibernation already on 23 September, *M. bechsteinii* one month later (20 October) and *M. nattereri* as late as 8 December; inversely, *M. nattereri* finished hibernation already in mid February, followed by *M. daubentonii* (9 March) and *M. bechsteinii* (22 March), whereas *M. emarginatus* hibernated until mid April.

The four studied species displayed also different thermal preferences at the onset and termination of hibernation (Fig. 6). While *M. emarginatus*, *M. bechsteinii* and *M. daubentonii* entered hibernation at T_a higher than 10 °C, *M. nattereri* initiated hibernation at $T_a = 4.5$ °C. Only *M. bechsteinii* emerged from hibernation at T_a higher than 10 °C, the other three species emerged at T_a between 4.5 °C and 10 °C. T_a . Only during the coldest months of the year (December to February), Hermann’s Cave was used as hibernaculum by all four species.

Post-arousal winter activity outside the cave in relation to T_a

Winter activity outside the cave expressed by post-arousal emergence flights during the species-specific hibernation period persisted throughout all months of hibernation (Fig. 7). Over the 205 days of the total hibernation period, we registered 179 emergence flights carried out by



Figs. 4, 5. Daily sums of emergence flights from Hermann’s Cave per bat day performed by the *Myotis* bats. 4 (top) – *Myotis bechsteinii*. 5 (below) – *Myotis nattereri*. Red: dates of the onset and termination of hibernation. From 23 September to 6 October camera 2 did not function.

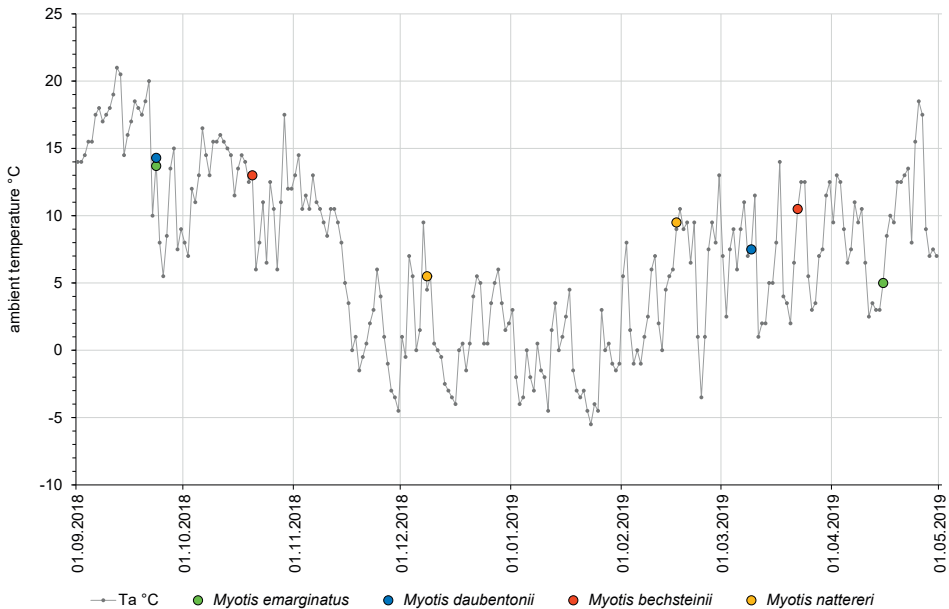


Fig. 6. Ambient temperatures (°C) and dates of the onset and termination of the hibernation periods of the four species studied.

individuals of the studied species during their species-specific hibernation period. The highest number of registrations (n=71) was recorded in *M. emarginatus*; during its short stay in the cave *M. nattereri* performed 59 emergence flights; and with 20 and 29 flights, respectively, *M. daubentonii* and *M. bechsteinii* exhibited the lowest winter activity outside the cave.

The numbers of post arousal emergence flights performed per bat day varied among species (Fig. 8). By far the most emergence flights were carried out by one or two individuals of a particular species. In *M. bechsteinii* and *M. daubentonii* we never registered more than two, but in *M. emarginatus* we recorded up to six and in *M. nattereri* up to eleven flights per bat day. A single evidence of synchronous emergence was obtained on 8 October when four *M. emarginatus* individuals left the cave within one minute.

The temporal distribution of emergence flights is shown in Fig. 9. In the first weeks of its hibernation period, *M. emarginatus* executed numerous post-arousal emergence flights scattered over the entire night time. From December to early January and again in February and April, several single individuals emerged around sunset which is the typical time for emerging from the summer roost to forage. In late February and March, *M. emarginatus* performed day-flights.

Myotis bechsteinii and *M. daubentonii* left the cave in all months except January. In both species the major part of emergence flights was registered at the end of the hibernation period. With one exception (*M. bechsteinii* in February), all flights occurred during night time. Busy activity outside the cave performed by *M. nattereri* was distributed over its entire hibernation period with lowest numbers in January. Only one post-arousal emergence flight occurred during day time.

Fig. 10 shows the post-arousal emergence flight-activity in relation to ambient temperature. Most flights of all species occurred at temperatures above 0 °C and – with the exception of *M. nattereri* – peaked at $T_a > 6$ °C in the first phase of hibernation (last decade of September to first decade of November). In the last phase of hibernation (mid February to March), flights of these species occurred also at lower T_a (1–4 °C). The temperature preference of *M. nattereri* differs distinctly from that of the other species. Most emergence flights occurred between T_a –5 °C and +6 °C.

DISCUSSION

Methodology

Phototrapping bats entering and leaving a cave is a superior method for monitoring these nocturnal animals and for investigating their hibernation phenology and hibernal activity. Until recently, monitoring of hibernating bats in a cave was mostly carried out by visiting the cave and counting visible specimens. However, as human access to all parts of a hibernaculum is possible only very rarely and most bat species prefer to hide in small crevices, the data obtained were incomplete and species determination was unreliable. Since the 1970s, chiropterological studies have taken advantage of technical innovations such as light barriers and cameras (DAAN 1973, LUBCZYK & NAGEL 1995, NAGEL & NAGEL 1997). Since then, the quality of phototrapping has been greatly improved (RYDELL et al. 2022) and is now widely used. It is non-invasive,

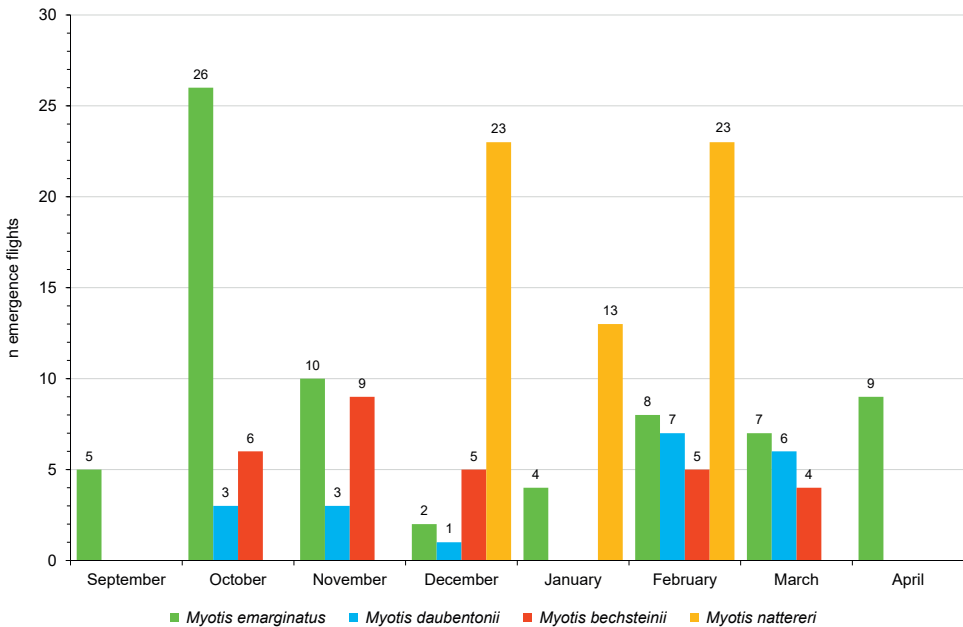


Fig. 7. Monthly sums of post-arousal emergence flights performed by the studied species during their species-specific hibernation periods. From 23 September to 6 October camera 2 did not function.

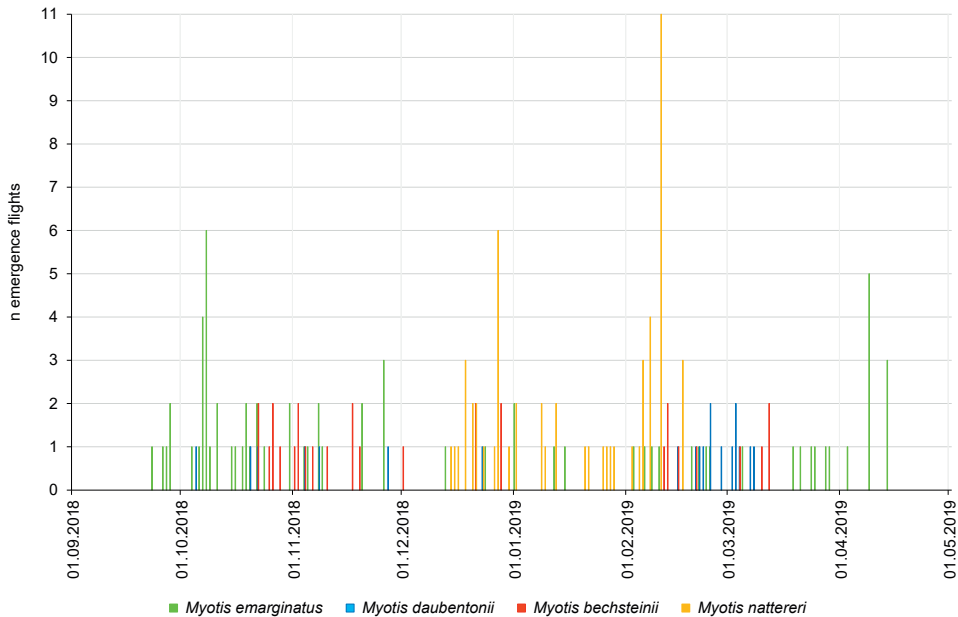


Fig. 8. Numbers of post-arousal emergence flights per bat day performed by the studied species during the species-specific hibernation periods. From 23 September to 6 October camera 2 did not function.

enables unambiguous identification of many species and supplies exact information on the arrival in and departure from the cave per second. The daily numbers of individuals of each species emerging from the cave can be determined by balancing the numbers of entering and emergence flights. However, phototrapping bats at the cave entrance during winter does not give information on hibernation intra-cave activities which may be at least ten times higher (DAAN 1973) than the extra-cave activities which makes an interpretation of the purpose of emergence flights, for instance as light sampling or feeding, impossible.

Factors shaping hibernation phenology and winter activity

Our results show that the four studied *Myotis* species hibernating simultaneously in the same cave pursued clearly different hibernation strategies. Among the factors shaping hibernation strategies such as the species origin, natural history, and life history traits, the availability of species-specific food (KÖRTNER & GEISER 2000) and the corresponding hunting strategies are – as a rule – the most important. They determine the amount of fat reserves gained in autumn and are thus the most important prerequisite for a long hibernation period.

All four species are arthropodivorous and are able to employ two hunting techniques: aerial hawking of flying insects and gleaning prey from surfaces, but differ in prey selection and seasonal use of hunting methods. As the low threshold for insect flights is 6 °C (HAYS et al. 1992), aerial hawking of flying insects is limited by low T_a , whereas hunting by skimming over

water surface and gleanng arthropods from terrestrial surfaces can be carried out also at lower ambient temperatures (PARSONS et al. 2003).

Post-arousal winter feeding can supplement low fat reserves needed to survive the winter. Winter feeding seems to be carried out by *M. emarginatus*, *M. daubentonii*, and *M. bechsteinii* at the beginning and end of the hibernation period at ambient temperatures above and a little lower than 6 °C (Fig. 10). Options for foraging at lower T_a are gleanng arthropods from substrates and eating cold-resistant insects that remain active and are able to fly at 0 °C or even lower (LEE & DENLINGER 1991). Replenishing fat reserves from time to time during hibernation seems to be the hibernation strategy pursued by *M. nattereri* (Fig. 10).

Myotis emarginatus

By exhibiting the almost longest hibernation period possible in Central Europe, *M. emarginatus* occupies a special position in the hibernation phenologies of temperate bats. In contrast to *Myotis daubentonii*, *M. bechsteinii* and *M. nattereri*, which are closely related, *M. emarginatus* is the only European representative of the Ethiopian genetic clade (STADELMANN et al. 2004). It differs in energy saving (SPITZENBERGER & WEISS 2021) and time keeping methods (SPITZENBERGER & WEISS 2020) from its congeners.

We assume that the unusually long hibernation period of *M. emarginatus* is achieved by following a strong circannual rhythm. In a six-year study it has been shown (SPITZENBERGER & WEISS 2020) that female *M. emarginatus* complete reproductive activities within 10–11 weeks

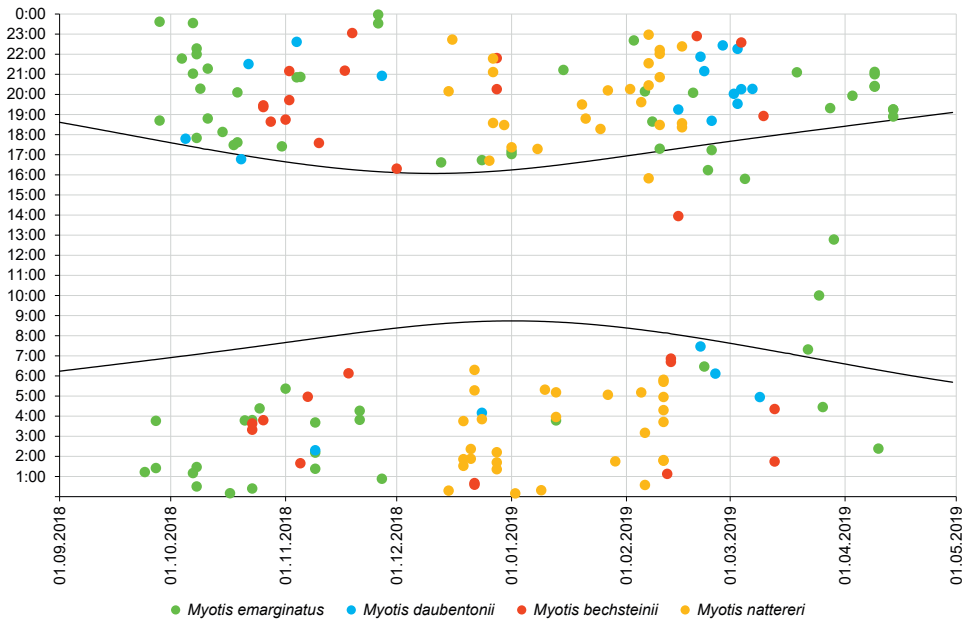


Fig. 9. Hourly registrations of post-arousal emergence flights per day during the species-specific hibernation periods in relation to sunset and sunrise (CET). From 23 September to 6 October camera 2 did not function.

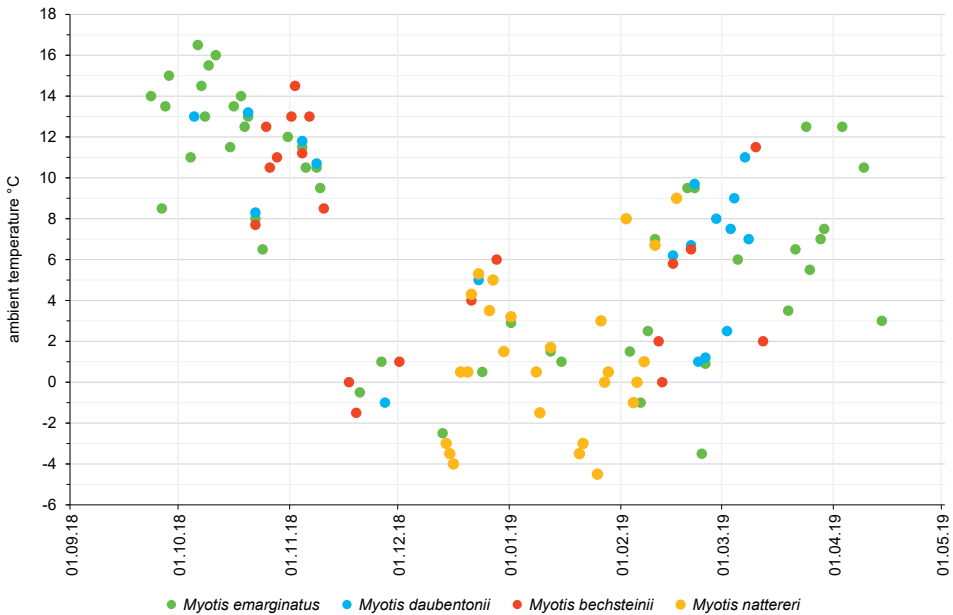


Fig. 10. Post-arousal emergence flights per bat day performed by the studied species during their species-specific hibernation periods in relation to T_a . From 23 September to 6 October camera 2 did not function.

and leave the nursery roost about the end of July. Before entering hibernation in September, a predictable time interval can be used for pre-hibernal accumulations of fat reserves that are large enough to survive the long hibernation period. By emerging from hibernation late (in mid-April) when disastrous catastrophes caused by premature emergence under adverse weather conditions (MEIER et al. 2022) are unlikely to occur, availability of abundant food is more secure than earlier in the year. During hibernation, *M. emarginatus* seems to be governed also by a circadian rhythm entrained by the photoperiod. This assumption is supported by the numerous post-arousal emergence flights occurring around sunset over almost the whole hibernation period (Fig. 9) which were used probably for light sampling.

Fecal analyses showed spiders as the dominant prey of *M. emarginatus* (BECK 1995, BAUEROVÁ 1986, GOITI et al. 2011). Spiders are an ideal food for bats. They are one of the most diverse and ubiquitous arthropod order (TURNBULL 1973) and have been reported to occur in peak numbers of more than 1000 individuals per m^2 (NYFELLER & BIRKHOFFER 2017). Many species are nocturnal (WARRANT & DACKER 2010) and are active throughout the year.

Soft short hairs on the trailing edge of the uropatagium of *M. emarginatus* have probably a sensory function for prey detecting and plucking web-building spiders from their webs (KERVYN et al. 2012). *Myotis emarginatus* hovers to glean spiders from surfaces (NORBERG & RAYNER 1987) and hunts insects in aerial pursuit (KRULL et al. 1991). It feeds opportunistically over dung pits and gleans flies sitting in large numbers on walls and ceilings in cow sheds (KRULL et al. 1991, BRINKMANN et al. 2001, STECK & BRINKMANN 2006, ZAHN et al. 2010, KERVYN et al. 2012). To obtain non-volant prey from the substrate in cluttered environment, it uses

hovering and gleaning as the hunting strategy. The fat reserves accumulated in autumn are so large that *M. emarginatus* can hibernate singly or in small groups (up to 30–35 individuals) in the warmest parts of the caves, preferably on the ceiling or in holes in the limestone (own observations). This is beneficial as bats with large energy reserves express only shallow torpor at relatively high body temperature (WOJCIECHOWSKI et al. 2007) and thereby avoid adverse torpor effects (BOYLES et al. 2007).

Myotis daubentonii

Myotis daubentonii is a cold-tolerant species that occurred in Central Europe during the same Holocene time interval as *M. nattereri*. Subfossil remains of *M. daubentonii* fall into the Atlantic and sub-Boreal chronozones (BLANT et al. 2010). Entering hibernation as early as *M. emarginatus* and emerging from hibernation more than one month earlier (Table 1), Daubenton's bats achieved the second longest hibernation period which was rarely interrupted by post-arousal emergence flights (Fig. 7). The onset and termination of hibernation are likely to be governed by the activity periods of its main prey, Chironomidae, which in turn seem to be determined by ambient temperature as has been suggested by a long-term study carried out in Nordrhein-Westfalen (MEIER et al. 2022).

The ability of *M. daubentonii* to gain fat reserves sufficient for a long hibernation period may be caused by (1) the specialisation in hunting Chironomidae and Trichoptera which are hawked a few centimetres above the water surface and gaffed with the feet (JONES & RAYNER 1988, KALKO & SCHNITZLER 1989). These water insects occur in high abundance over the whole activity period of *M. daubentonii*. Besides the insects emerging from water bodies, *M. daubentonii* hunts a great variety of other insects by aerial hawking; (2) the capability to hunt during 90% of the night (RIEGER 1996) and the independence from ambient temperature during hunting. Hunting has been observed between 3.5 °C and 25 °C (RIEGER 1996) and even during weak frosts (−3.3 °C; CIECHANOWSKI et al. 2007).

Myotis bechsteinii

Myotis bechsteinii is a thermophilous species that appeared in Austria after the last glacial about 13–11 thousand years BP. During the Holocene climatic optimum (10–4 thousand years BP) it was very abundant in the large mixed forests that covered Central Europe (BAUER 1987, BAUER & SPITZENBERGER 2002, BLANT et al. 2010). In comparison with *M. daubentonii*, the hibernation period of *M. bechsteinii* was shorter and the onset and termination occurred considerably later (Table 1). Ambient temperatures at the onset and termination of hibernation were high (>10 °C). Only few post-arousal emergence flights occurred at temperatures lower than 6 °C (Fig. 10).

We assume that the hibernation phenology of *M. bechsteinii* is associated with its origin in the warm huge, primeval forests existing in the Holocene optimum. The adaptation of *M. bechsteinii* to a warm climate and favourable roost conditions existing in large primeval forests is still perceptible by the preference for roosting sites located in warm mature oak and beech forest (DIETZ & KIEFER 2014) at low altitudes. Further evidence is provided by its sedentary habits that show a tendency to remain in the breeding area (SCHLAPP 1990) and to occupy small core hunting areas that are near to the day roost (DIETZ & PIR 2009). The relatively late end of hibernation may be influenced by the time at which trees come into leaf and enable insect availability in the forest.

In contrast to cold-adapted species, *M. bechsteinii* hibernates singly or in small groups in the warmest part of the caves in open spaces and crevices (ČERVENÝ & BÜRGER 1987, BAAGØE 2001). This indicates that the bats had stored large fat reserves before hibernation. The diet is

extraordinarily diverse. WOLZ (2013) determined prey of 25 arthropod families. Besides opportunistic feeding on flying insects, it prefers non-volant prey that is gleaned from vegetation, and also from the ground by using prey-generated sounds. This enables activity at lower T_a than is possible when hunting flying insects. A sample of faeces collected in Bavaria contained, besides a few volant insects, 81.5% of Dermaptera, Araneae, Opiliones, Chilopoda and larvae of Lepidoptera and of diurnal flies which rested on substrate during the night (WOLZ 1993).

Myotis nattereri

M. nattereri is a cold-tolerant bat species (BLANT et al. 2010) that lived in Austrian caves already at the turn between Pleistocene and Holocene (FLADERER 2000, SPITZENBERGER 2002). It keeps hibernation short and does not store enough body fat in autumn to survive the winter, but replenishes its fat reserves by interrupting hibernation for hunting. It risks high mortality in case of long adverse weather spells when feeding is hampered (REUSCH et al. 2019), but benefits from using less torpor. Given the considerable trophic niche overlap with *M. emarginatus* and *M. daubentonii*, *M. nattereri* benefits also from feeding during winter when the competitors remain in the hibernaculum (Fig. 10).

In line with the fact that the pre-hibernal increase of body mass in *M. nattereri* begins as late as in the second half of October and reaches a maximum at the end of November (KRZANOWSKI 1961), this bat species started hibernation in Hermann's Cave in the first decade of December and stayed there only during the coldest part of the winter (December–February; Fig. 7). In each month, the bats left Hermann's Cave (sometimes in groups; Fig. 8) intermittently (Fig. 10) for foraging. Foraging by *M. nattereri* during winter has been reported already by SWIFT (1997) and HOPE et al. (2014).

M. nattereri uses a large variety of hunting habitats (ARLETTAZ 1996, SWIFT 1997, SIEMERS et al. 1999, SMITH & RACEY 2008) and several techniques for hunting its extraordinarily diverse prey. *M. nattereri* is able to pursue prey quadrupedally after landing (SWIFT & RACEY 2002) and has access to silent, suspended prey very close to vegetation (e.g. spiders, and caterpillars on thread) by using frequency-modulated search signals of a very broad bandwidth (ARLETTAZ 1996, SIEMERS & SCHNITZLER 2000). Bristle-like hairs on the trailing edge of the uropatagium most probably have a sensory function for prey detection and capture, and a mechanical function for brushing prey off the substrate (HORÁČEK & HANÁK 1983, ARLETTAZ 1996, CZECH et al. 2008, ANDREAS et al. 2010). Dependent on the study site and time of the year, prey items were Trichoptera, Chironomidae, Brachycera and Nematocera, many of them diurnal, Hymenoptera, Hemiptera, Coleoptera and non flying arthropods such as spiders and Isopoda, Opiliones, and Dermaptera (BAUEROVÁ & ČERVENÝ 1986, GREGOR & BAUEROVÁ 1987, BECK 1995, SHIEL et al. 1991, SWIFT 1997, HOPE et al. 2014, KRÜGER et al. 2014).

Hibernation behaviour of *Myotis nattereri* is typical for bat species hibernating in non-stable hibernacula (DAAN 1973, TURBILL & GEISER 2008, HOPE & JONES 2012, BERNARD et al. 2021). Of the studied species, it shows the lowest affinity to caves, has been found hibernating in rock crevices, various underground sites and rubble (DIETZ & KIEFER 2014), in hollows in trees and in walls of buildings (ČERVENÝ & HORÁČEK 1981). It is also very flexible in choosing nursery roosts (LAUFENS 1973, ČERVENÝ & HORÁČEK 1981, SMITH & RACEY 2018).

The fact that *M. nattereri* did not shift the onset of the hibernation periods during the long-term study conducted in Nordrhein-Westfalen in contrast to *M. daubentonii* (MEIER et al. 2022) indicates that the hibernation phenology of *M. nattereri* is not governed by ambient temperature but rather by a circadian activity rhythm entrained to the photoperiod persisting over the whole period as already published by HOPE & JONES (2013).

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