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HIBERNATION TEMPERATURES IN SEVEN SPECIES OF SEDENTARY BATS (CHIROPTERA) IN NORTHEASTERN EUROPE

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Abstract. During 30 years of observations carried out in over 1,000 underground and semi-underground bat hibernation sites in Estonia, air temperature was measured near sleeping bats. In 1978, the 'lower critical temperature of hibernation' (LCT) was determined for two boreal bat species, *Plecotus auritus* and *Eptesicus nilssonii*. The LCT was defined as the mean value calculated on the basis of temperatures at which animals of a certain bat species awoke as a result of temperature decrease at their sleeping sites. For the first species, the LCT was -2.24°C, while for the second it was -3.13°C. During the past 20 years, we have registered new records of minimum hibernation temperatures for the following four sedentary bat species: *Eptesicus nilssonii* (-5.3°C), *Myotis dasycneme* (-2.5°C), *Myotis brandtii* (-2.5°C) and *Myotis nattereri* (-1.0°C). The highest temperatures (up to +10.5°C) were recorded near bats sleeping in cellar-type shelters in October and November. As a result of research, we concluded that the upper limit of 'hibernation temperatures' in boreal bats is variable depending both on the species and the site. Based on temperature measurements and observations of bat activity during the year, we propose +8°C to mark the upper temperature limit of hibernation for seven bat species under study.
Key words: bats, hibernation, temperatures, shelters, Estonia

Introduction

During the second half of the 20th century, hibernation conditions of bats were studied in northeastern Europe (Ling 1953; Poots 1956; Strelkov 1958, 1969, 1971; Randla 1969; Masing 1980, 1981b, 1982, 1983, 1984, 1987, 2004; Masing *et al*. 1982; Masing & Buša 1983; Buša 1984, 1986; Masing & Poots 1984; Liiva & Masing 1987). From those studies it appeared that seven species of bats known to hibernate in this region choose relatively humid and cool conditions for hibernation, which often occur in underground spaces such as caves, mines, tunnels, cellars and bunkers. Four species: pond bat (*Myotis dasycneme*), Brandt's bat (*Myotis brandtii*), whiskered bat (*Myotis mystacinus*) and Natterer's bat (*Myotis nattereri*) preferred temperatures between 0 and +8°C for hibernation, whereas Daubenton's bat (*Myotis daubentonii*), brown long-eared bat (*Plecotus auritus*) and northern bat (*Eptesicus nilssonii*) were sometimes found hibernating below 0°C (Ling 1953; Strelkov 1958; Randla 1969; Masing 1981b; Masing & Buša 1983). It was also revealed that severe frost, which at times occurs in the regions close to the Baltic Sea, can awaken bats, force them to change hibernation sites and even make them leave the roosts (Masing 1981b, 1987; Liiva & Masing 1987). The results of temperature studies carried out in bat hibernation sites in Europe are summarised in well-known handbooks (Schober & Grimmberger 1987, 1997).

Temperatures measured at bat hibernation sites are different for the same bat species hibernating in the same type of underground shelters in different parts of Europe. Thus, it was discovered that in caves of the Ural Mountains the same bat species hibernated at 1–2°C lower temperatures than they did in the areas near St. Petersburg (Leningrad) (Strelkov 1958). It was also found that the mean temperatures measured at hibernation sites of three species of *Myotis* (*dasycneme*, *daubentonii* and *brandtii/mystacinus*) were 2.1°C higher in the Netherlands compared with the same type of underground shelters in Estonia (Masing 1982). Bats hibernating at lower temperatures benefit energetically (Ling 1953; Strelkov 1971) and are therefore able to hibernate up to 6–8 months in a row. Such behaviour is common in sedentary bats living in northeastern Europe.

During the severe frost in Estonia in the last days of December 1978, when air temperatures fell to -30°C and even lower, a special study was carried out in a large abandoned cellar in the city of Tartu (Gunpowder Cellar, later transformed into a restaurant). This study ascertained the 'lower critical temperature of hibernation' (LCT) for two boreal bat species, *Plecotus auritus* and *Eptesicus nilssonii*. The LCT was defined as the mean value calculated on the basis of temperatures at which animals of a certain bat species awoke when temperature decreased at their sleeping sites. In the first species, the LCT was -2.24°C, while in the second species it was -3.13°C (Masing 1981b).

Observations of *Myotis* bats hibernating at low air temperatures, however, can rarely be carried out under natural conditions. This is partly because these bats choose relatively protected sites for hibernation where temperatures seldom fall below the critical level and because prolonged frost capable to influence the microclimate in deep underground shelters does not occur very often. Thus, LCTs for five species of *Myotis,* hibernating in deep underground rooms like old mines, tunnels and caves, are still poorly known.

The present article summarizes our observations carried out in underground and semi-underground shelters in Estonia during a 30-year period. It also compares our results with those received in the other parts of northeastern Europe.

Material and methods

Observations carried out throughout Estonia during the whole bat hibernation period from October to April

The study was carried out throughout Estonia beginning from January 1976 to February 2006. During the observation of over 1,000 underground and semi-underground shelters, over 4,000 temperature measurements were taken near sleeping bats. Ordinary hand torches or headlamps were used to maintain orientation in dark underground spaces, as well as to find bats. To measure temperatures, either mercury thermometers (such as OW-1-1989, GOST 215-73 TL-2) or VAISALA HM 34 humidity and temperature meter (in 2003–2004) were used. With both types of equipment, the measuring accuracy was ±0.1–0.2°C. Air temperature was measured within a few centimetres from bats, including animals sleeping in crevices. When bats were hibernating out of hand reach (e.g. over 2 m high, either on the wall or below the ceiling of an underground site), thermometers were temporarily attached to wooden sticks (Fig. 1).

Figure 1. A mercury thermometer attached to a wooden stick to measure air temperature near hibernating bats. *Myotis brandtii* (on the left) and *Eptesicus nilssonii* (on the right) sleeping at -1.7°C (January 2006; photo by Matti Masing).

During 2001–2004, we carried out observations of hibernating bats in three Estonian counties (Harjumaa, Raplamaa and Lääne-Virumaa), inspecting basements and cellars situated in old manors and castles, and other shelters of a similar type. In the course of this work, we measured both air temperature and humidity near hibernating bats. Because part of the study was carried out in October and November, which is the beginning of the hibernation season of sedentary bats in Estonia, we could measure the highest temperatures available in these underground sites during the hibernation period. In this season, over 600 temperature measurements were taken in cellar-type underground shelters. At the sites where the highest temperatures were measured, like +10.5°C near *Myotis nattereri*, bats were not fully asleep as their bodies slightly moved when the animals were lighted by a hand torch.

Observations carried out in an underground tunnel near Tallinn

In January 2006, we had a rare possibility to continue observations of bats hibernating at low temperatures. Between 18 and 22 January, five days in a row, air temperatures in northern Estonia varied from -29 to -13°C. Frost penetrated into underground rooms of abandoned mines and tunnels near Tallinn where five species of boreal bats were known to hibernate. Such a situation provided us with a unique possibility to observe hibernating *Myotis* bats at extremely low temperatures. A section of a relatively straight underground tunnel (248 m long, 2–4 m wide, 1.7–4 m high), a part of an abandoned mine at Ülgase (20 km east of Tallinn), was chosen for the study. In this tunnel, low air temperatures were known to occur during severe frost. The main entrance of the tunnel faces northeast and is about 3 m in diameter allowing free air circulation between the mine and the outside world (Fig. 2). The end of the tunnel is connected with the main system of the mine, which has several additional entrances in other places.

Within the study area, the bats were sleeping either in holes or crevices, or openly on the walls, mostly at the heights of 1.7–2.7 m from the tunnel floor.
Three visits were made to the tunnel: on 21 and 23 January and 5 February 2006, always in the late evening. During the first two visits at the end of a 5-day-long frost period, mainly temperatures below zero were recorded in the study area. During the first visit, the wind outside the mine was blowing from the east, while in the tunnel a relatively strong air flow was coming from the direction of the tunnel entrance. The air flow constantly brought cold air into the tunnel and cooled the tunnel walls down. During the third visit, however, the wind outside the mine was blowing from the north, while the air in the tunnel (especially below the ceiling) moved in the opposite direction. Thus, during our last visit the tunnel was much warmer with air temperatures between +0.5 – +4.5°C.

Results

Observations of sleeping bats in midwinter, with special attention to low air temperatures

During observations in midwinter, when temperatures outdoors are usually the lowest, we often found bats hibernating below zero, especially in shelters with open entrances and/or relatively thin ceilings. These bats mostly belonged to *Eptesicus nilssonii*, which often chooses less protected hibernation sites such as caves, tunnels, bunkers and abandoned cellars with open entrances, and tolerates temperatures down to -5.5°C. In some underground sites, such as cellars, we found *Plecotus auritus* hibernating at freezing temperatures down to -3.7°C (Masing 1981b).

Figure 2. Main entrance of the underground tunnel where observations were made in January and February 2006 (January 2004; photo by Matti Masing).

In search of bats hibernating close to their lower temperature limits, we sometimes found single individuals of *Myotis dasycneme*, *Myotis daubentonii*, *Myotis brandtii* and *Myotis nattereri* sleeping in the wall crevices of abandoned cellars situated in western and northern parts of mainland Estonia at temperatures close to 0°C. *Myotis nattereri* was once found even at -1.0°C, measured at its sleeping site in a crevice between limestone bricks in the ceiling of an abandoned cellar, 15 km west of Märjamaa (3 March 2001). The animal surely survived such a low temperature, as it was not found there later. In March 2000 and 2001, single individuals of *Myotis mystacinus* were sleeping on concrete walls of bunkers in northern Hiiumaa, in both situations at +1°C.
On several occasions, however, bats were not able to survive such low air temperatures, which usually occur either in January or February. During the winters, when temperatures below -15°C lasted for many consecutive days, bats hibernating in shelters with large openings were often found frozen. They belonged mostly either to *Myotis daubentonii*, *Myotis nattereri* or *Plecotus auritus* (Fig. 3). *Eptesicus nilssonii*, the species most often found in open cellars, seems capable of surviving such frost, because it usually awakes and leaves the roost when the temperature falls below the critical level (Masing 1981b, 1987; Liiva & Masing 1987). For instance, in January 2003, one bat, probably belonging to this species, was observed flying into a haystack of a barn in southeast Estonia when the outside temperature dropped to -20°C. In cold winters, this species often forms groups consisting of 3–10 animals, obviously to avoid damage caused by low tem-

Figure 3. Victims of severe frost: *Plecotus auritus* and *Myotis nattereri* found dead in the crevices of relatively open limestone cellars near Märjamaa after the temperature fell below -3°C (February 2003; photo by Matti Masing).

peratures. In open cellars, especially those situated in ruins, these bats also hide in narrow crevices where they sleep at freezing temperatures, sometimes for weeks and even months. After the spells of frost, northern bats can be often found in cellars, bunkers, caves or mines sleeping at -2 or -3°C. When the environment is wet enough, the bats hibernating below zero are surrounded by ice crystals (Fig. 4).

In December 1978, one individual of *Eptesicus nilssonii* was observed waking up from hibernation and leaving its sleeping site at the Gunpowder Cellar in Tartu at -5.5°C (Masing 1981b). For a decade this temperature remained the lowest one recorded at the hibernation site of this species in northeastern Europe, but this bat actually did not hibernate at -5.5°C, because at this temperature it left the site. In January 1988, we observed two individuals of *Eptesicus nilssonii* sleeping side by side in a relatively open place at Piusa, cave 3 (Lutsar *et al*. 2000). During three days of observation, the following air temperatures were measured near these animals quietly sleeping below the ceiling, 4.5 m from the floor: 28 January -5.3°C, 29 January -5.3°C and 30 January -5.1°C. As both bats were missing from the site later in the season, we concluded that they had survived those negative temperatures. The latter observation finally proved that northern bats hibernating in natural conditions indeed tolerate -5°C at least for three consecutive days.

Observations of sleeping bats in autumn before true hibernation

It is well known that before true hibernation bats are relatively active, spending much time in search of both food and roosting sites where they go to hibernate (Ryberg 1947; Strelkov 1971). Abandoned cellars and basements with large openings, situated either within or near the buildings of earlier castles and landlord manors, present a common type of the underground roost for sedentary bat species throughout Estonia. As a result of the 1905 rebellion of peasants against landlords, when buildings in many manors were burnt down, but also for other reasons such as destruction and fires after 1905, a large number of manor buildings are now in ruins. These ruins provide excellent possibilities for bats to use numerous holes and crevices, especially in basements and cellars (Masing 1980, 1981a, 1983; Masing *et al*. 1982; Masing & Poots 1984). Particularly cellars built of limestone bricks, found in northern and western parts of the country, are of major importance to bats, because both the building material and the architecture of these shelters allow them to resist natural destruction caused by water, ice and gravity, and because both microclimate and crevices between the bricks provide excellent conditions for hibernation (Fig. 5). Such basements and cellars, especially when situated deep under the ground, are similar to natural caves, which many bat species recognize as preferred shelters (Fig. 6). Over 1,000 roosting sites of this type are known in Estonia, but conditions in each of them are different depending on their volume, degree of destruction, number and size of entrances, number and placement of crevices and other factors. Some of those underground rooms have been renovated and are now used as storage rooms, exhibition rooms or restaurants and in those cases they have become unsuitable for bats.

If the entrances of the cellars are large, then warm air coming from the outside during the summer warms up the underground rooms. As a result, temperatures like +15°C can be measured in these sites in July and August. In September, the temperatures inside and outside the cellars become even. Bats start using these

Figure 4. Eptesicus nilssonii hibernating in a wall crevice of a basement at Järvakandi, with ice crystals surrounding its sleeping place (February 2003; photo by Matti Masing).

Figure 5. Ruins of the main building of Salajõe manor in northwestern Estonia, a transient shelter of sedentary bats (November 2000; photo by Lauri Lutsar).

Figure 6. A fully underground and relatively warm and damp shelter situated in the ruins of a manor house near Rakvere, resembles a natural cave. Five bat species hibernate here (October 2003; photo by Matti Masing).

rooms as daytime sleeping sites mostly since mid-October when air temperature in the cellars is higher and more stable compared with conditions outside. Each year, from mid-October to mid-November, bats use these cellars as transient roosts (Gaisler 1979; Masing 1984) before moving over to true hibernation sites. Because the entrances of these cellars are large, the rooms cool down relatively fast after the outside temperature falls below 0°C. That is why *Myotis* bats and *Plecotus auritus* very often cannot hibernate in such cellars after November or December. For some bats these sites become ecological traps where they die due to low temperatures if they do not leave the shelter in time (Fig. 3). Temperatures measured near sleeping bats at the beginning of hibernation period in October and November are given in Table 1.

Observations made in an underground tunnel near Tallinn

During our visits to the tunnel near Tallinn in January and early February 2006, all bats were found sleeping, but many of them changed their hibernation sites between our visits. It was interesting to observe changes in the clustering behaviour of bats as a result of temperature change in the tunnel. For instance, two clusters of *Eptesicus nilssonii* (4 and 5 individuals together) were hanging on the tunnel wall during the first two visits when air temperature near these clusters was -2.3 – -0.4°C. During our third visit on 5 February, with relatively warm conditions observed at the same place (+3.5 – +4.3°C), both clusters were missing. Instead we found the tunnel walls covered with solitary northern bats, often at distances of 1–2 m from each other and close to the sites where their clusters had been previously found.

21 January. Air temperature outside the tunnel -13.7°C, wind from the east. Hibernating bats were found in the tunnel section between the points of 36 and 240 m, measured from the entrance. Within the study section, air temperatures measured at a height of 2 m from the floor were (all below zero): a) 35 m from the entrance -7.5°C; b) 55 m from the entrance -2.7°C; c) 170 m from the entrance -2.3°C and d) 248 m from the entrance -1.0°C. Cold air from the outside was flowing into the tunnel through the entrance directed to the northeast. Most bats found in the study area were hibernating between -4.7 – -1.0°C. Four *Myotis* bats found in the crevices were hibernating at +0.2°C (Figs 1 and 7, Table 2).

23 January. Air temperature outside the tunnel -7.3°C, wind from the southeast. Hibernating bats were found in the tunnel section between the points of 36 and 240 m, measured from the entrance. Air temperatures 2 m from the floor were (all below zero): a) 35 m from

Table 1. Temperature ranges (°C) near bats hibernating in cellar-type roosting sites in three Estonian counties from mid-October to mid-November.

Species	Harjumaa	Raplamaa	Lääne-Virumaa	Total
Period	2001–2002	2001–2003	2003	2001–2003
Number of shelters observed	66	142	101	309
Air temperature near bats:				
*Myotis dasycneme**			4.6–9.0	4.6–9.0
Myotis daubentonii	2.2–7.3	1.0–7.5	3.4–8.0	1.0–8.0
*Myotis brandtii**		7.5–10.0		7.5–10.0
Myotis nattereri		1.7–7.5	2.5–10.5	1.7–10.5
Plecotus auritus	2.2–7.6	1.0–9.6	1.6–9.7	1.0–9.7
Eptesicus nilssonii	1.0–7.3	1.0–8.2	3.6–8.4	1.0–8.4
Total of all species	1.0–7.6	1.0–10.0	1.6–10.5	1.0–10.5

** – temperatures near Myotis dasycneme and Myotis brandtii were measured only in one cellar concerning each of these species* the entrance -2.5°C; b) 55 m from the entrance -2.8°C; c) 170 m from the entrance -0.9°C and d) 248 m from the entrance -1.0°C. The air in the tunnel was not moving much, probably because of the southeastern wind. In the tunnel, air temperature had increased by 1–2°C, compared to the situation two days earlier. All bats found in the study area were hibernating between -2.0 – -0.2°C.

5 February. Air temperature outside the tunnel -14.0°C, wind from the north. Hibernating bats were found in the tunnel section between the points of 22 and 240 m, measured from the entrance. Air temperatures 2 m from the floor were (all above zero): a) 35 m from the entrance +0.5°C; b) 55 m from the entrance +1.5°C; c) 170 m from the entrance +3.8°C and d) 248 m from the entrance +4.5°C. On 5 February, the tunnel was much warmer than during the previous visits. Warm air penetrated into the tunnel from the main part of the mine as a result of reverse wind direction compared to the situation on 21 January. This was probably caused by the penetration of the northern wind into the mine from the other northern entrances. All bats were hibernating between -0.3 – +4.5°C.

Figure 7. Myotis daubentonii (on the left) and *Myotis brandtii* (on the right) sleeping together at -1.1°C. In both animals, ice crystals are covering dorsal fur (January 2006; photo by Matti Masing).

As a result of 111 temperature measurements taken near the bats hibernating in an underground tunnel near Tallinn during and after a 5-day-long frost period, it became clear that these bats had to tolerate temperatures below zero for about one week. The mean values of temperatures taken during the three selected days were about 0°C in all five bat species studied (Table 2, last column). During the study in the tunnel in January 2006, the following new records of low temperatures measured near hibernating bats were registered: *Myotis dasycneme* hibernated at -2.5°C (two individuals together), whereas *Myotis brandtii* hibernated at -2.0°C (two individuals separately).

Conclusive remarks on the observations made in the underground tunnel near Tallinn

Between 18 and 22 January 2006, relatively strong frost occurred in northern Estonia, during which outside tem-

Table 2. Air temperature (°C) near hibernating bats on three different dates characterizing temperature conditions of five bat species in an underground tunnel during and after a 5-day-long frost period in January 2006.

Species	21 January	23 January	5 February	From 23 January to 5 February
	Range (mean), N*	Range (mean), N*	Range (mean), N*	Range (mean of three days), N*
Myotis dasycneme	-2.5–0.2 (-1.32), N = 5	-0.9 – -0.3 (-0.58), N = 4	-0.3–3.8 (1.70), N = 5	-2.5–3.8 (-0.07), N = 14
Myotis daubentonii	-2.0–0.2 (-1.04), N = 9	-1.0 – -0.2 (-0.56), N = 7	-0.3–4.5 (2.55), N = 6	-2.0–4.5 (0.32), N = 22
Myotis brandtii	-2.0 – -1.0 (-1.62), N = 12	-1.1 – -0.3 (-0.86), N = 10	2.5–3.8 (3.40), N = 9	-2.0–3.8 (0.31), N = 31
Plecotus auritus	-2.5 – -1.7 (-2.17), N = 3	-1.1 – -0.9 (-1.00), N = 2	3.8, N = 1	-2.5–3.8 (0.21), N = 6
Eptesicus nilssonii	-4.7 – -1.0 (-2.27), N = 13	-2.0 – -0.3 (-0.66), N = 14	0.9–3.5 (2.97), N = 11	-4.7–3.5 (0.01), N = 38
Total of all species	-4.7–0.2, N = 42	-2.0 – -0.2, N = 37	-0.3–4.5, N = 32	-4.7–4.5, N = 111

N – number of bats studied, number of measurements taken* peratures fluctuated between -29 – -13°C. As a result, in a 248 m long tunnel connected with an old mine situated near Tallinn air temperatures fell several degrees below zero. In this tunnel, a regular hibernation site of five bat species, the lowest temperatures probably occurred on 21 January, when they dropped down to -2.5°C in the middle part of the tunnel. At that time, three species of *Myotis* and one of *Plecotus* were found hibernating at temperatures between -2.5 – -2.0°C, while *Eptesicus nilssonii* was found even at -4.7°C. After 23 January, temperatures in the tunnel began to rise relatively fast, probably because outside temperatures were close to 0°C and because warm air (up to +8°C) penetrated into the tunnel from the main part of the mine.

As awakening bats were not observed in the tunnel on 21 January and as the temperature in the tunnel had stopped falling by that time, it was impossible to calculate the 'lower critical temperatures of hibernation' for any of the bat species observed. After 23 January, temperatures in the tunnel raised above zero relatively quickly, restoring normal hibernation conditions for bats. Consequently, negative temperatures caused by a 5-day-long frost period lasted in this tunnel only about seven days. Such frost probably did not influence bats too much as the temperature did not fall below the critical level at most hibernation sites.

The study carried out in an underground tunnel near Tallinn shows that in the case of large entrances both factors, low air temperature and wind direction, significantly influence microclimate in underground hibernation sites of bats. If frost is prolonged and the wind gets in temperatures in the tunnels can fall below 'lower critical temperatures of hibernation' known in boreal bat species. Ascertaining LCT values for *Myotis* bats, however, was not possible in the present study. This means that further research is needed to reach this special target.

Discussion

As a result of long-term observations carried out at underground bat roosting sites in northeastern Europe, temperature preferences of hibernating bats can be summarised (Table 3). The lower temperature limits given in Table 3 indicate the lowest values measured for the species concerned. Upper temperature limits of hibernation are less certain, because boreal bats can get torpid at various temperatures below +15°C (personal observations carried out at various shelters), which does not always mean hibernation (i.e. prolonged sleep without taking food). Sleeping bats can be found in relatively great numbers in underground shelters such as old mines and cellars already in August (Strelkov 1971; Liiva & Masing 1987; Masing, in press). This is the period when bats move around a lot, keep on foraging and are not yet preparing for hibernation. Consequently, relatively high temperatures measured near sleeping bats at that time of the year cannot be considered temperatures of hibernation.

The main hibernation period of sedentary bats in Esto-

Table 3. Temperature ranges (°C) near hibernating bats in northeastern Europe according to different literature sources. Hibernation period lasts from October to the end of April. Concerning temperatures not given in brackets, bats were considered hibernating at least during 24 hours.

Species	Ling 1953	Strelkov 1958	Masing 1981b, 1982 (sometimes)	Schober & Grimmberger 1997* (sometimes)	Masing & Lutsar, original data from Estonia (sometimes**)
Myotis dasycneme		2–7	2–7.5	0.5–7.5	-2.5–8 (9.0)
Myotis daubentonii	-3–7	1–7	-2–11	3–6 (-2–8)	-2.0–8
Myotis brandtii	6***	1.5–7***	0–7.5	3–4 (0–7.5)	-2.0–8 (10.0)
Myotis mystacinus				2–8	1–5****
Myotis nattereri		4–7	-0.5–7	-0.5–7	-1.0–8 (10.5)
Plecotus auritus	-1.5–7	0–8	-2.5–9.5 (-3.7)	2–5 (-3.5)	-2.5–8 (-3.7–9.7)
Eptesicus nilssonii	-2.8–6	-3–6	-3.5–8.5 (-5.5)	1–5.5 (-5.5–7.5)	-5.3–8 (-5.5–8.4)

** – this handbook covers also central, southern and western parts of Europe; ** – maximum temperatures were measured (often in transient roosts) from mid-October to mid-November (data from Table 1); *** – perhaps Myotis brandtii (the sibling species M. brandtii and M. mystacinus were not separated at that time); **** – in Myotis mystacinus temperature measurements were taken only near five animals hibernating in four underground sites, all between January and March (one basement, one bunker and two sand mines)* nia and neighbouring areas occurs between October and April when most bats cannot find sufficient food (Ling 1953; Randla 1969; Strelkov 1969, 1971; Masing 1984). Our nighttime observations in Estonia, in which ultrasound detectors were used, showed that during this 6–7-month period sedentary bats rarely flew outside the roosts. Instead, they were sleeping in underground rooms and other shelters. Consequently, there is sufficient evidence to consider the latter about 7-month period as the main period of bat hibernation in Estonia and elsewhere in northeastern Europe. Thus, temperatures measured near bats sleeping either in hibernation roosts or transient shelters from early October to late April we consider 'hibernation temperatures'. Between October and April, night temperatures in northeastern Europe rarely exceed +8 – +10°C. And when they sometimes do, then there is usually not enough insect food available for bats. Boreal bats seldom forage below +8°C; instead they get torpid and stay in their daytime shelters (Ryberg 1947). We have observed this phenomenon especially in September, before sedentary bats start hibernation in Estonia. During short and cool nights in May and June, many bats are still foraging when air temperature drops to +4°C or even lower (Masing & Siivonen 2005; pers. observ.). But in September, the flight activity of bats often stops when the temperature falls below +8°C. In the latter season, bats are active mostly during the first hours of darkness in the evening when flying insects are still relatively abundant. In October, the flight activity of bats in typical foraging sites near water is so low that it is hard to find a flying bat even when using very sensitive ultrasound equipment, like a Pettersson D240 bat-detector (pers. observ.).

From the above-said we conclude that about +8°C can be considered the upper temperature limit of bat hibernation in northeastern Europe. This is often also the highest temperature occurring in deep underground rooms throughout the year. In Estonia, this temperature, which is close to the mean annual temperature outside, occurs in old mines and in some of the tunnels of Peter the Great Sea Fortress near Tallinn. The latter sites are regularly used by five species of bats for hibernation (Ling 1953; Randla 1969). But the upper temperature limit (like +8°C) is not, and cannot be, preferred by bats during the whole hibernation period, because in this case their body fat will be used up too quickly to survive until next spring (Ling 1953).

In both transient and hibernation shelters, bats are sometimes found sleeping above +8°C (Table 1). Usually this happens at the beginning of hibernation period, but sometimes also in spring and summer. During the transient period, annually occurring between the high activity period in summer and the low activity period in winter, bats often fly out when the night is warm, but they sleep for several days when the weather is unsuitable for feeding. Boreal bats certainly cannot hibernate at temperatures like +8°C or higher throughout the hibernation period and in northeastern Europe they are rarely found hibernating at such temperatures in midwinter. That is why the temperatures higher than +8°C in the last column of Table 3 are given in brackets.

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Septynių sėslių šikšnosparnių (Chiroptera) rūšių žiemojimo temperatūra šiaurės rytinėje Estijos dalyje

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Santrauka

Trisdešimties metų oro temperatūros stebėjimai buvo atlikti šalia įmigusių šikšnosparnių daugiau kaip 1,000 požeminių ir pusiau požeminių šikšnosparnių žiemaviečių Estijoje. 1987 m. žemiausia kritinė žiemojimo temperatūra buvo nustatyta dviems šiaurinėms šikšnosparnių rūšims – *Plecotus auritus* ir *Eptesicus nilssonii*. Žemiausia kritinė žiemojimo temperatūra buvo išreikšta kaip vidurkis temperatūrų, prie kurių tam tikros rūšies gyvūnai atsibusdavo, nukritus oro temperatūrai žiemavietėse. Buvo nustatyta, kad -2,24°C yra pirmosios rūšies žemiausia kritinė temperatūra, o antrosios – -3,13°C. Per dvidešimtį metų žemiausia kritinė žiemojimo temperatūra buvo nustatyta šioms sėslių šikšnosparnių rūšims: *Eptesicus nilssonii* (-5,3°C), *Myotis dasycneme* (-2,5°C), *Myotis brandtii* (-2,5°C) ir *Myotis nattereri* (-1,0°C). Aukščiausia temperatūra (iki +10,5°C) buvo užregistruota spalio ir lapkričio mėnesiais šalia šikšnosparnių žiemojančių rūsio tipo slėptuvėse. Tyrimų rezultatai parodė, kad aukščiausia žiemojimo temperatūros riba šiaurinėms rūšims yra skirtinga kiekvienai rūšiai ir priklauso nuo žiemavietės tipo. Remdamiesi temperatūrų matavimo duomenimis ir šikšnosparnių aktyvumo per visus metus stebėjimais, darome prielaidą, kad +8°C yra aukščiausia žiemojimo temperatūra septynioms mūsų tirtoms šikšnosparnių rūšims.

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