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Hide and seek: A pilot study on day roosts in autumn and hibernacula for Vesper bats in southeast Norway

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Abstract

1. Bats constitute >20% of all terrestrial mammal species in Norway (12 resident species, 7 on the national Red list). Yet, the knowledge of their distribution, population trends and potential threats in Norway is very limited. Little is known about the locations of hibernacula (overwintering sites) in Norway. Hibernacula are a vital part of the life history strategy of bats, and information about the location and characteristics of such sites is much needed for knowledge-based management and conservation.

2. The main objective of the study was to identify hibernacula and roost sites of northern bats (*Eptesicus nilsonii*), Daubenton's bats (*Myotis daubentonii*) and brown long-eared bats (*Plecotus auritus*) during autumn, the period of the year when the bat activity is reduced and eventually ends in Norway.

3. 15 bats were captured using mist nets and harp traps in Nittedal municipality (Akershus county), and fitted with radio transmitters. Radio telemetry was used to identify day roost sites and to observe the movements of the radio tagged individuals. Stationary bat recorders (with adjacent temperature loggers) were deployed at three sites: in front of a barn cellar, a mine and a scree, to automatically observe the activity of the bats. Hibernacula surveys from seven mines in southeast Norway (1981-2017) were supplemented with new field registrations in 2017-2018, and the dataset was analyzed to determine which factors affect species composition and location of bats in human-made mines.

4. The use of radio telemetry resulted in identification of 11 different roost sites; of northern bats (2), Daubenton's bats (1) and brown long-eared bats (9), but no new hibernacula. Roost site use varied substantially between individuals, with some bats being stationary in one roost, whilst others changed roost every day. Activity recorded by use of automatic bat loggers showed that the bats were less active later in the autumn. Analysis of the hibernacula survey data showed that the mines in Sognsvann, Djupdal, Engelstadtjern and Røysåsen had substantial increases in total number of individuals over the survey years, Spenningsby had a slight increase, whereas Alnsjøen and Engelstadvang showed no significant changes. As both the inside and outside temperature of the mine at Sognsvann increased, the number of bat individuals decreased. Both the whiskered bat/Brandt's bat and the Daubenton's bat hibernated deeper into the mines than the northern bat and the brown long eared bat.

5. Radio telemetry worked well for locating autumn roost sites, but proved challenging for finding hibernacula during autumn; despite considerable efforts and resources, it yielded little empirical data. A need for further research on possible overwintering sites is evident to ensure evidence-based management and conservation of bats.

Introduction

Bats (order: Chiroptera) are one of the most successful mammalian orders in the world, and probably the most diverse (Altringham, 1996). They constitute >20% of all terrestrial mammal species in Norway (12 resident species, 7 on the national Red list) (Henriksen et al., 2015). Bats show functional and taxonomic diversity, are widely distributed, and provide key ecosystem services like culling insect populations, hunting pest species, and serve as pollinators and important bioindicators (Barlow et al., 2015; Jones, 2009).

Norway has, since 1993, acceded to The Agreement on the Conservation of Populations of European Bats (EUROBATS http://www.eurobats.org/). Contracting Parties in EUROBATS have taken on obligations to protect all 53 European bat species through legislation, education, conservation measures and international cooperation. Many European bat species have experienced declining populations (Mickleburgh et al., 2002). Factors threatening bat populations include habitat loss and fragmentation, roost and hibernacula disturbance, pesticide contamination, health issues, and changes in land use practices (Stone et al., 2013). Knowledge about the distribution, population trends, and threats the bat species that occur in Norway are facing, is very limited (Isaksen, 2009), and research has so far been limited to the fjord landscape of western Norway (Michaelsen, 2016; Michaelsen et al., 2011; Michaelsen et al., 2013) and the northern parts of Norway (Frafjord, 2013; J. Rydell et al., 1994). Hence, there is a need to fill these knowledge gaps for scientists and wildlife managers to ensure evidence-based management and conservation of bats.

Most bat species show some degree of specificity regarding their roosting habitats, including the use of caves, rock crevices, trees, man-made structures and cavities constructed by other animals like wood peckers (Ngamprasertwong et al., 2014). Day roosts are vital for the survival of the bats, and provide sites for mating, rearing young (maternity colonies), social interactions, protection from the weather, predation and parasitism (Ngamprasertwong et al., 2014).

Torpor, used on a daily basis for energy budgeting, or for long periods of hibernation, is an important component of the life history strategy of bats in both temperate and tropical regions (Altringham, 1996). Torpor is defined as a controlled reduction of body temperature, reduction of O_2 consumption, heart rate, breathing rate, metabolic rate, and includes an ability to arouse spontaneously (wake up to change hibernacula, change position within the hibernacula, hydrate, copulate etc.). Hibernation is an extended form of torpor, often used in response to a reduction in food supply or a fall in ambient temperature over a longer period of time (Altringham, 1996).

Bats in Norway feed exclusively on invertebrates, whereby most are insects that they catch in flight at night (Isaksen, 2009). Temperatures below 10ºC are likely to constrain insect abundance (Czenze et al., 2017). During winter, insect abundance is therefore reduced to near zero in northern latitudes. Thus, the bats must migrate or hibernate to cope with this seasonal food shortage. Hibernation allows bats to survive for long periods using relatively little energy (Perry, 2013). The best sites for hibernation have high humidity, which reduces evaporative water loss during hibernation (Perry, 2013), and stable temperatures that remain within a relatively narrow range, typically between 2 and 10ºC (Meyer et al., 2016). Bats exposed to temperatures from 0 to - 6.5ºC begin to suffer from exhaustion resulting from energy over-expenditure, and exposure to temperatures from – 9 to - 15ºC leads to severe overcooling, and the bats will eventually freeze to death. Overwintering bats seek to avoid areas with temperatures above 5 ºC for prolonged periods, probably because it is difficult to maintain sufficiently low levels of metabolic processes required for long-term torpor at such temperatures (Smirnov et al., 2008).

Isolated house walls, cellars, wells, stone bridges, caves, mines, bunkers and rock screes can all provide good overwintering sites in northern latitudes (Isaksen, 2009). In Norway, hibernating bats are mostly observed in mines/caves, but the locations of most bats during winter in Norway is still unknown (Isaksen, 2009). The observed bats during winter in Norway represent only a small fraction of the populations observed during summer (van der Kooij et al., 2012). It is likely that some bats use crevices and rock screes as hibernacula (Frafjord, 2007). Buildings could also provide suitable habitats for overwintering, but are normally too warm, too cold or too dry, for bats to use them as hibernacula (Isaksen, 2009). Michaelsen, Olsen & Grimstad (2013) found that northern bats and whiskered bats *Myotis mystacinus* used rock scree and crevices in rock walls as roosting sites when bat activity stopped and during winter conditions.

During a short period in late summer and early autumn, bats from the same or different species may congregate in front of underground sites such as mines and screes. This phenomenon is known as swarming. Some individuals stay only for a single night, and individual and species turnover can be high. Classically, swarming sites were thought to serve as information centers, where juveniles gained knowledge about suitable hibernacula, accompanied by their mothers (Veith et al., 2004). It is now widely believed that swarming also has a mating function in many temperate zone bats, and that this can facilitate gene flow between isolated populations (Furmankiewicz et al., 2006; Piksa, 2008; van Schaik et al., 2015; Veith et al., 2004). Such swarming sites may support large populations from large geographical areas, and thus need special protection (Furmankiewicz & Altringham, 2006).

The main objective of the study was to identify roost sites, roost site characteristics and hibernacula during autumn, the period of the year when the bat activity is reduced and eventually comes to an end in Norway. I used radio telemetry and automatic bat recorders for this purpose. I wanted to find out whether radio telemetry is a good method for finding roost sites and hibernacula during autumn in Norway. I also wanted to find out if automatic logging of echolocalization calls can give additional information about bat activity and swarming behaviour.

The core study area contained a number of manmade mines, rock screes and crevices in rock walls, and at least some of these will have suitable temperatures and humidity levels for hibernating bats, whilst also serving as potential swarming sites (Michaelsen et al., 2013). In addition to the telemetry and echolocalization calls data collected in the core study area, I also used survey data of hibernating bats from abandoned human-made mines in southeast Norway, outside the core study area. This dataset was used to analyze which factors determine species composition and location of bats in mines in southeast Norway during hibernation.

Methods

Permits and preparations

Before initiating the field season, the necessary permits were obtained to radio-tag bats from the Norwegian Food Safety Authority (Mattilsynet), capture bats in the field from the Norwegian Environmenal Agency (Miljødirektoratet) and to use frequencies on the 142 MHz band for bat radio-telemetry studies from the Norwegian Communications Authority (Nasjonal kommunikasjonsmyndighet). All project participants, who were going to be in direct contact with bats, underwent rabies vaccination before handling bats, because bat rabies has recently been detected for the first time in mainline Norway (Moldal et al., 2017).

Study period, areas and species: radio telemetry and batlogger data collection

The field work for the data collection with radio telemetry and automatic bat echolocation call recorders was carried out in the autumn (August 23. – late November 2017). Data collection was primarily done in Nittedal and Gjerdrum municipalities in Akershus county, but we also radio-tracked bats in Oslo, Skedsmo, Sørum and Lunner municipalities. Within the study area, settlements and agricultural areas dominate the landscape at low elevations, whereas mainly coniferous forests but also some mixed forests dominate the surrounding landscape at higher elevations. The species that were radio tagged and tracked in this study were northern bats, Daubenton's bats, and brown long-eared bats.

Trapping, body measurements and tagging

The bats were trapped at irregular intervals at different locations using either mist nets or harp traps (the latter was only used on two occasions) (Plate 1, Table A1). After capture, bats were temporarily kept in bird holding bags and fed meal worms to compensate for the loss of foraging time and to calm the bats down before tagging.

Body mass of the captured individuals was measured to the nearest 0.1 g using an electronic balance with a cardboard tube (which the bat could cling on to on the inside), and forearm length was measured to the nearest 0.1 mm with a Vernier caliper (Plate 1). Age class and sexual status was determined from a combination of the following characters: fusion of the phalangeal epiphyse (in the wings), the presence of a chin-spot (for *M. daubentonii*), the pelage color, the shape and appearance of the nipples (in females), the shape of the belly and weight of the animal (in females) and the color of the epidydimes (in males) (Haarsma, 2008). Sex was determined from inspection of the genitals.

Bats were equipped with BioTrack Pip4 or PicoPip radio tags with light to medium potting (Biotrack, UK). The tag weight ranged from 0.30 to 0.48 g, i.e. 3.73 – 5.16% of the bat's body mass. As a rule-of-thumb, tag weight should not exceed 5% of the body mass, to not impair the bats' flight ability. A patch of fur between the shoulder blades of the animals were cut short with a surgical scissor before the radio tags were mounted with glue (Hautkleber) between the shoulder blades. Surrounding hair was then glued on top of the transmitter.

Tracking radio tagged individuals

Radio tagged bats were tracked using Sika receivers (Biotrack, UK) and handheld directional three-element Yagi antennae (Biotrack, UK). Several observers cooperated to cover large areas of land on foot. Holterkollen (455 m a.s.l.) and Varingskollen (546 m a.s.l.) were high elevation sites that we used as vantage points in the early stages of searching. A non-directional whip antenna mounted on the car roof was also used to cover larger areas more quickly. In one case, we tracked and relocated bats from an airplane. The airplane tracking was carried out by experienced personnel (pilot Ole-Jørgen Kjellmark, research technician Roger Meås, NINA and senior researcher Ole-Gunnar Støen, NINA).

The first bat was caught and radio tagged on August 23, and the last individual was radio tagged on October 16. Due to the long nights of the autumn, following the bats throughout the whole night was not feasible with the available personnel (1-3 people). The daily fieldwork routine was therefore to track radio tagged bats during daytime to find roost sites, and thereafter track the bats during hunting until around midnight. We used a combination of singular bearings, cross-bearings, triangulations, visual observations and bat detectors (Magenta Bat5) to determine bat locations during tracking. We noted down the geographic position (using a hand-held GPS, Garmin 64st), signal strength, bearing, gain and interference for every observation.

Automatic logging of echolocation calls

To monitor the activity of bats at locations where we expected or knew that there would be bat activity (i.e. 24-hour periods and general activity throughout the autumn season), we deployed three bat recorders, which recorded and stored echolocation calls (BatCorder, EcoObs) at three different locations: outside a barn cellar, at a scree at Holterkollen, and outside an abandoned mine (Table 1). Along with each bat recorder, we deployed a temperature logger (Gemini TinyTag), which recorded the air temperature every 10 minutes. The three bat recorders were deployed on September 15/17/20, respectively, and recollected on November 8/11/13. The batteries were changed and the data were transferred to a laptop at regular intervals during this period. Automatic loggers have been found to show different shortcomings raising concerns about the use of automated classifiers for identification to species level (Jens Rydell et al., 2017), and thus we focused purely on the total bat activity (i.e., activity of all bat species).

Table 1. Batlogger information: Geographic positions (UTM coordinates), elevation, total number of bat echolocation recordings, deployment period and time of the last recording.

Site	Location	UTM32V_E	UTM32V_N	Meters a.s.l.	Total recordings	Deployment period	Last recording
Barn cellar	Nordre Berg	605094	6662048	152	2173	15.09. - 08.11.	22:40 31.10.
Scree	Holterkollen	607084	6657549	267	132	17.09. – 11.11.	18:53 14.10.
Mine	Spenningsby	606555	6662598	230	240	20.09. – 13.11.	23:58 27.10.

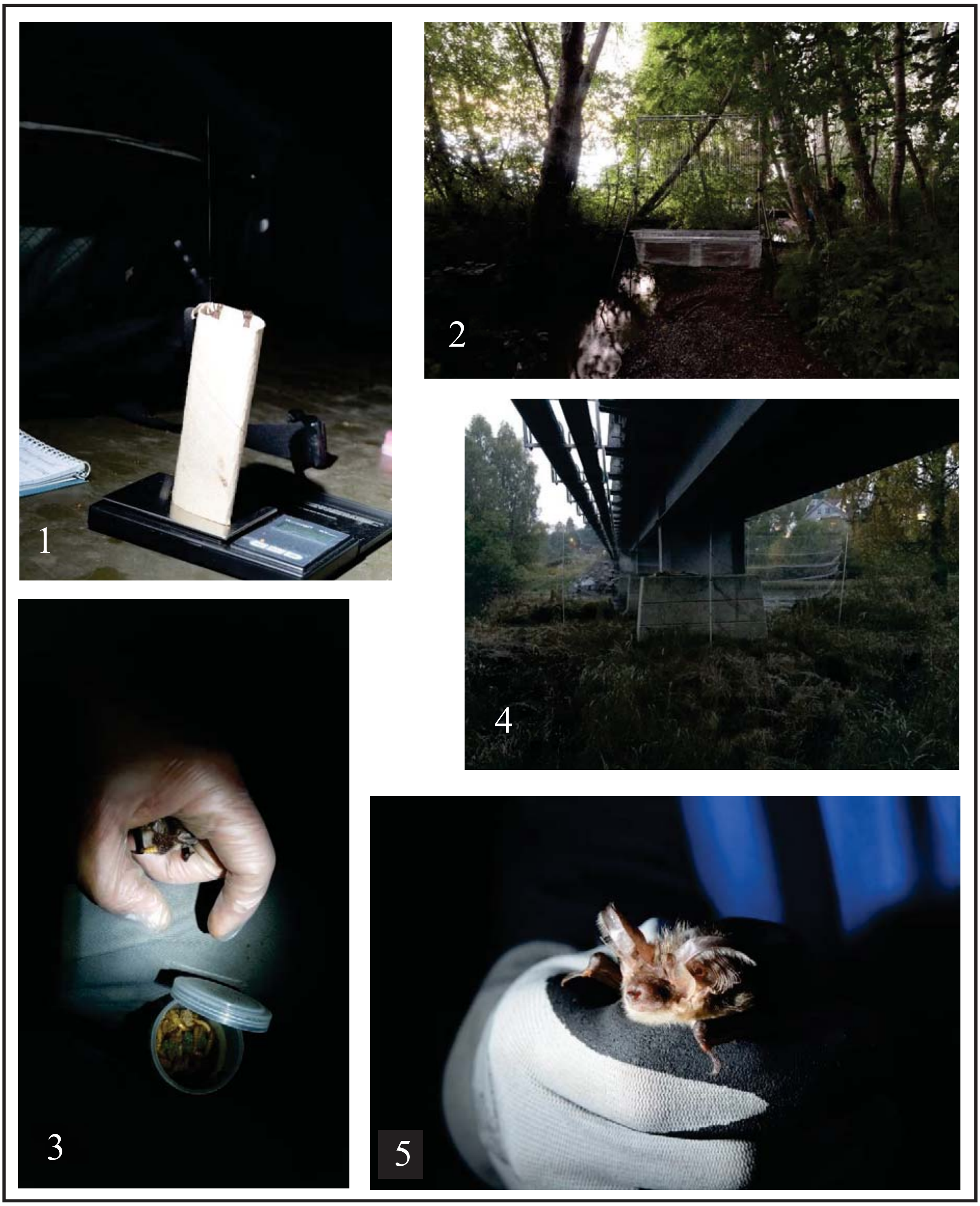

Plate 1. (1) Body weight measurement. Bat hanging inside cardboard tube (Photo: Jeroen van der Kooij). (2) Harp trap setup during the summer field period (Photo: Jeroen van der Kooij). (3) *P. auritus* being fed meal worms after capture (Photo: Jeroen van der Kooij). (4) Mist net setup at Li bridge during the autumn field period (Photo: Kristian F. Kristiansen). (5) *P. auritus* moments before release (Photo: Jeroen van der Kooij).

Hibernacula data from mine surveys

I was given access to a mine survey dataset collected by members of the Bat Group of the Norwegian Zoological Society (Norsk Zoologisk Forening Flaggermusgruppen, NZFF). Before analysis I had to extract the data from hand-written field note books and enter the data into an Excel spreadsheet. This dataset contains yearly hibernacula-registrations from seven mines dating back to 1981 at different locations in southeast Norway (Fig. 1, Table 2). One of the mines (Sognsvannsgruven, Oslo) have had fortnightly registrations throughout the hibernation season (late October – early May) for each survey year, whereas the six others have had one survey round (one day) per year (December-February). Due to this large difference in number of observations per mine, the Sognsvann mine data was analyzed separately. Drawings of the mines' two-dimensional spatial configurations are found in the appendix (Fig. A4 – A10). The registrations were done by groups of observers (1-10 people, depending on the size of the mine). Walls, roofs, cracks, drilling holes etc. were checked thoroughly with flashlights. For every bat observed, the following information was recorded: species, distance to the entrance, whether it was solitary or in a cluster of bats and − sporadically − if there was condensation on the animal or not. *Myotis brandtii* and *M. mystacinus* cannot be distinguished during hibernation, and thus they have been registered as one group during the surveys.

In addition to this NZFF dataset, I carried out fortnightly registrations of the mine at Sognsvann throughout the winter of 2017-2018. The first count was carried out on November 24, and the last count on April 18. On November 24, one temperature logger (Gemini TinyTag and EasyLog EL-USB-1) was deployed outside the mine, 30 m from the mine entrance (2 m above the ground), and six loggers were deployed inside the mine, at increasing distances from the entrance (10, 20, 30, 40, 50 and 60 m) and at varying heights: 185, 180, 175, 180, 130 and 30 cm (end of the mine) above the mine floor. These temperature loggers recorded the temperature once per hour throughout the survey period. The logger at 10 meters also registered humidity.

The very first systematic registration of bats in the mine at Sognsvann was done in 1987, and there have been in total 255 registrations since (until this winter). This mine is located approximately 350 meters southwest of the Sognsvann lake and 470 meters west-northwest of the Norwegian School of Sport (Norges Idrettshøgskole, NIH), in an area frequently used for recreational purposes. The mine has one entrance, and the full length is 62 meters (Table 2). The mine used to have another entrance in the far end, which has been closed off with rocks, but it is still penetrable for air to flow through. The mine at Alnsjø has one entrance, and a stream of water that runs through the entire mine (drain tube for Alnsjøen lake). This mine has the largest maximum depth of the mines included in the analysis. The mine at Engelstadvang has three entrances, one of which is on a flat surface, whereas the other two are on top of the hill, forming what can resemble a chimney. The mine at Engelstadtjern is very close to Engelstadvang, has five entrances, and differing depths of water can be found throughout the mine, especially near entrance one (Fig. A10). This mine is also connected to other mines, and it has tunnels on different levels, contributing with many different microhabitats for bats. The mine at Spenningsby has one entrance and is located just south of Bergstjern (Fig. 2). The mine at Djupdal has one entrance, and is known as "langøregruva" ("the brown long eared bat mine"), due to its high proportion of brown long eared bats. The mine at Røysåsen also has one entrance and is located in Hurum municipality (Fig. 1).

Table 2. Characteristics of the human-made mines searched for hibernating bats: geographic position, elevation, total length (including all branches/side tunnels), maximum depth (meters from entrance(s) to the furthest point away from any entrance), number of entrances, number of registrations, time period of the registrations, and mean ± standard error number of bat individuals recorded per survey.

Mine	County	Municipality	UTM32V_E	UTM32V_N	Meters a.s.l.	Length (m)	Max depth (m)	No. of entrances	Registrations (surveys)	Survey years	Individuals (Mean ± SD)
Sognsvann	Oslo	Oslo	595809	6649096	250	62	62	1	255	1987-2018	4.39 ± 2.35
Alnsjø	Oslo	Oslo	603200	6649800	239	663	663	1	19	1995-2015	7.43 ± 2.65
Engelstadvang	Akershus	Nannestad	604000	6672500	475	857,5	232	3	22	1996-2017	19.88 ± 4.51
Engelstadtjern	Akershus	Nannestad	603286	6672953	475	800,5	258.5	5	22	1996-2017	19.65 ± 3.96
Spenningsby	Akershus	Nittedal	606555	6662598	230	210	114	1	17	1996-2017	8.34 ± 3.29
Djupdal	Akershus	Nittedal	604800	6667000	370	74	53	1	8	1996-2015	3.52 ± 1.20
Røysåsen	Buskerud	Hurum	582100	6611900	180	180	145.5	1	29	1981-2017	11.73 ± 4.07

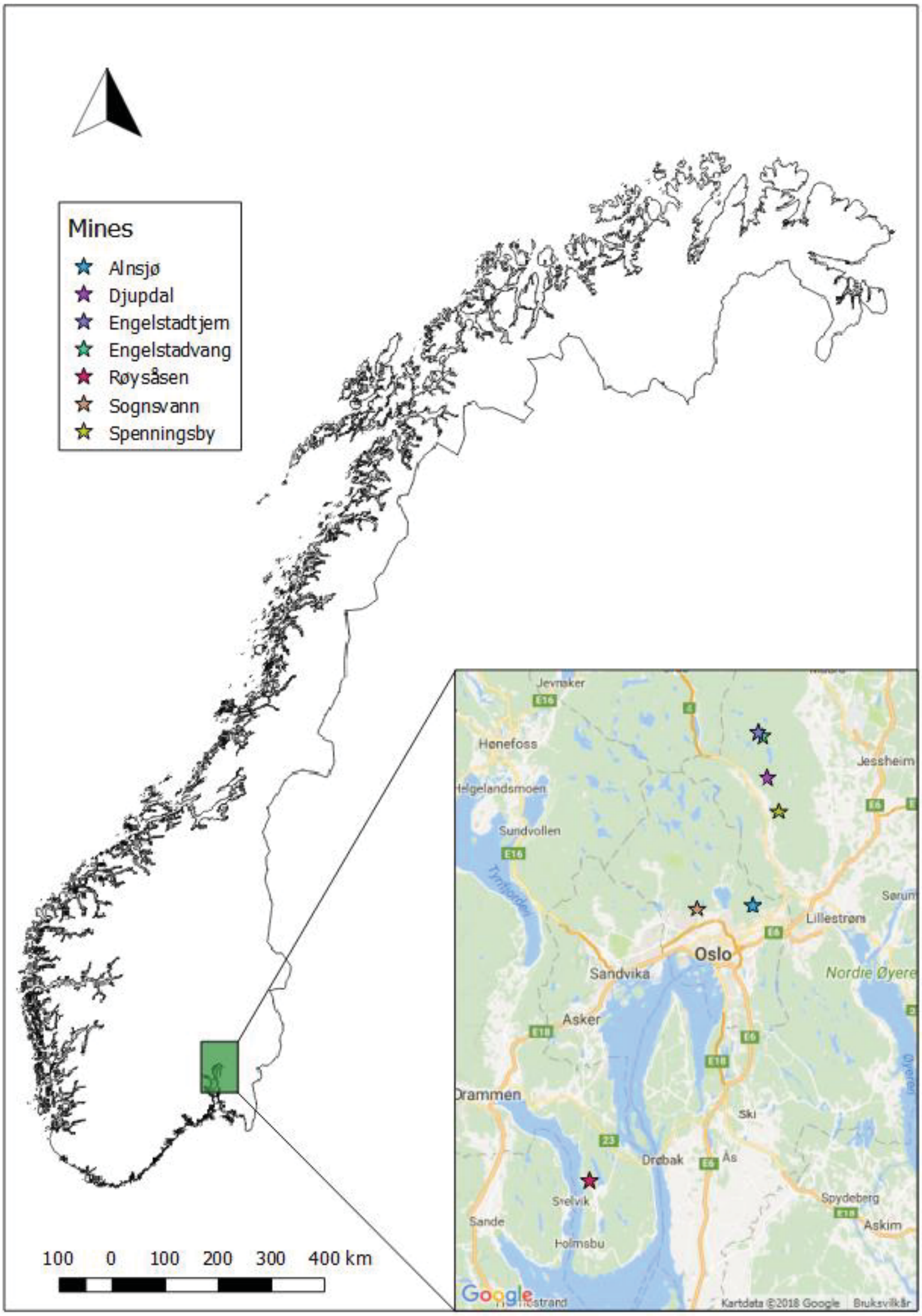

Figure 1. Mine overview map. Zooming in on the green section shows the location of the seven mines (the stars on the enlarged section map) visited during the bat surveys.

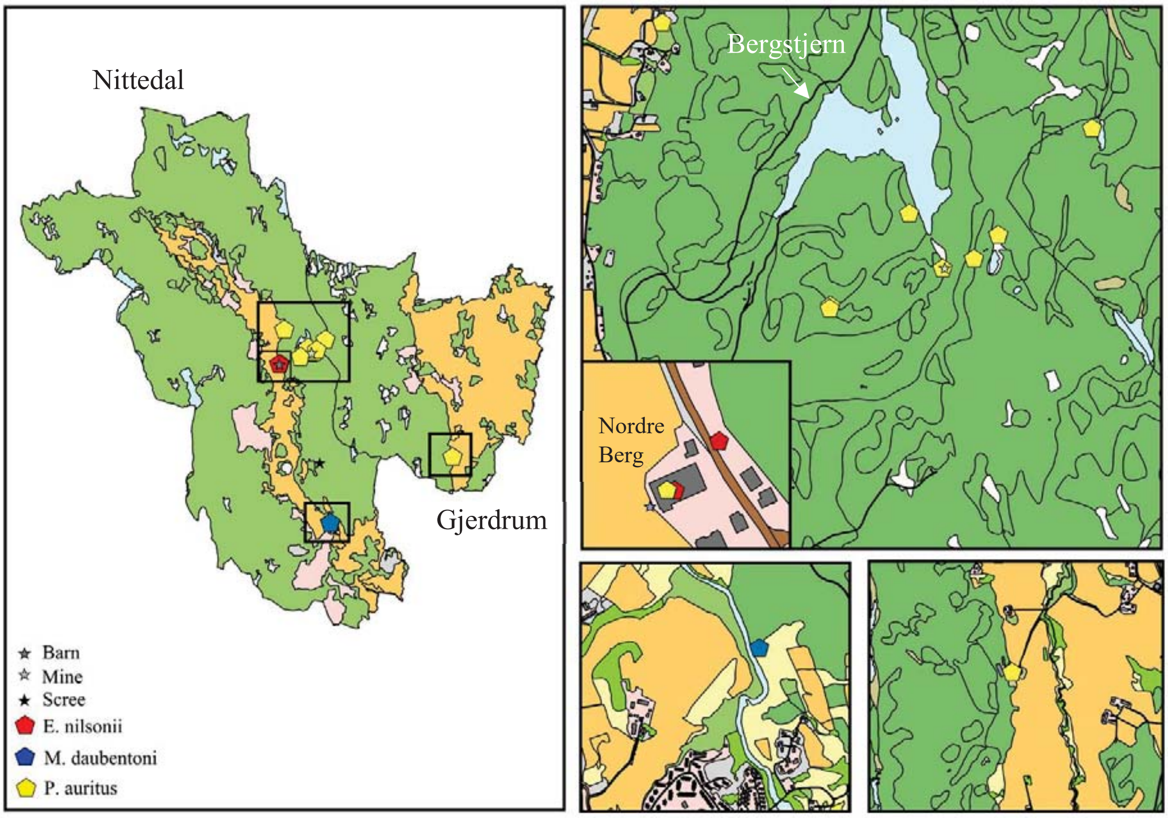

Figure 2. Map of the study area for the radiotelemetry and batlogger (echolocations) data collection, showing Nittedal and Gjerdrum municipality, including autumn roost sites and batlogger deployment locations. Symbols: pentagons denote roost sites (red = northern bats, blue = Daubenton's bats, yellow = brown long eared bats), and grey stars denote batlogger locations.

Climate data

Snow depth and temperature data for the mines were extracted from www.senorge.no, developed by the Norwegian Water Resources and Energy Directorate (Norges vassdrags- og energidirektorat, NVE). The maps used for data extraction are interpolated raster maps, i.e. they are estimations of surface values at unsampled points based on known surface values of surrounding points (weather stations). The temperature data was extracted to match the mine survey observations, and were mean daytime temperatures from the days of the observations. The snow cover data was extracted to match the mine survey observations, and were total snow depth from the days of the surveys. Temperature data for the mine at Sognsvann in the years 1987-2017 (November-May) were recorded during most of the surveys using a stationary thermometer deployed outside of the mine and/or a hand-held thermometer which was brought inside the mine (approximately 15 m inside) for measurement.

Data management and analysis

The dataset was subjected to initial exploratory analyses following Zuur et al. (2010) to check for outliers and collinearity between candidate explanatory variables and to explore relationships between response variables and explanatory variables (Zuur et al., 2010). I used the statistical software R (R Core Team, 2017) for all exploratory and statistical analyses.

To analyze the relationship between number of bats recorded in the mines and time (years), a generalized linear model (GLM) was fitted with ‘maximum number of individuals observed per year’ as the response variable. Number of individuals was a count response variable, so I assumed Poisson distribution of errors and used the log link function to fit GLMs. Year was included as the explanatory variable.

To analyze if the number of bats individual observed was influenced by temperature or snow depth in the Sognsvann mine, a GLM were fitted with number of individuals as the response variable, log link function and Poisson distribution of errors. Temperature (inside temperature for the mine at Sognsvann), snow cover (factor with three levels; <30 cm, 30-60 cm and >60 cm deep) and the interaction between temperature and snow cover were included as explanatory variables.

To analyze if the number of bats observed in the mine surveys was influenced by temperature or snow cover in the other mines, a generalized linear mixed model (GLMM) was fitted with number of individuals as the response variable, log link function and Poisson distribution of errors, using the “lme4” package in R (Bates et al., 2015). Temperature, snow cover and the interaction between these were included as explanatory variables. In addition, mine identity was fitted as random effect. We carried out model selection by backward elimination (Crawley, 2013). Explanatory variables were retained in the final model if their influence on the response was statistically significant ($P<0.05$). Yet, since there was a large among-mines variation in the relationship between number of bats observed and temperature and snow cover, I decided to analyze this relationship separately for each mine with GLMs.

To analyze if the bat species differed with respect to their position relative to the entrance of the Sognsvann mine, I fitted a GLM with distance to entrance as the response variable (i.e. number of meters from the entrance), log link function and Poisson distribution of errors. Species was included as the explanatory variable.

To analyze if the total number of individuals changed over time in the other mines, linear models were fitted with total number of individuals as the response variable. Year was included as the explanatory variable.

To analyze the species’ differences in distance to entrance in the other mines, a GLMM was fitted with distance to entrance as the response variable, log link function and Poisson distribution of errors. The “drop1” function (Bates et al., 2015) was used to determine that mine identity had a significant effect on the distribution of bats (distance to entrance), and thus the relationship was analyzed separately for each mine. Pairwise comparisons tests were used to determine the species differences.

For making maps and plotting Kernel density plots, I used the Geographical Information System QGIS (QGIS Version 2.18.10). To plot Kernel density plots in QGIS, coordinates from on-site plots, strong signals and triangulation plots were extracted from all field observations. 50%, 75% and 95% percentiles were used to determine home ranges. The packages used for this purpose were: “adehabitatHR”, “adehabitatL”T, “adehabitatHS”, “adehabitatMA” (Calenge, 2006), “sp” (Pebesma et al., 2005), “rgdal” (Bivand et al., 2017) and “raster” (Hijmans, 2017).

Three Batcorder programs were used for automatic echolocation data analysis: bcAdmin (Version 2.35 (1549)), bcAnalyze (Version 1.16 (305)) and batIdent (Version 1.03), running the package “kernlab” from the randomForest library (Liaw et al., 2002) (© ecoObs, Volker Runkel, 2009 – 2014). To predict total number of bat recordings over time, GLMs were fitted with total number of bat recordings as the response variable for the three sites. I assumed Poisson distribution of errors and used the log link function to fit the GLMs. Night (date) was included as the explanatory variable.

Table 3. *Myotis*, *Plecotus* and *Eptesicus* bats radio tagged during the autumn field work period in 2017, Bat ID = latter numeric of the individual tag frequencies (142.XXX MHz), % weight = relative weight of transmitter in relation to body mass, Age class: Ad = adult; Juv = juvenile; NA = age not determined, Roosts = number of daytime roosts utilized during the field period (+ denotes that the individual used at least one day roost we were unable to locate), Days tracked = number of days the bat was tracked after radio tagging (* denotes that it was the number of days between the first and last signal capture, i.e. the bat was not tracked every night).

Date of capture	Species	Bat ID	Sex	Forearm length (mm)	Mass (g)	% weight	Age class	Roosts	Days tracked*	Expected battery (days)
23.08.2017	*P. auritus*	395	M	38,5	7,30	4,52	Ad	6	6	12
23.08.2017	*P. auritus*	106	M	40,4	7,80	4,23	Juv	2	11	12
24.08.2017	*M. daubentonii*	281	F	39,3	11,00	3,73	Ad	0	6	20
28.08.2017	*E. nilsonii*	285	M	37,4	9,00	4,96	NA	2	14	16
28.08.2017	*P. auritus*	342	F	39,8	9,08	4,67	NA	1	6	27
12.09.2017	*P. auritus*	147	M	38,5	6,33	4,74	Ad	1+	3	10
12.09.2017	*P. auritus*	331	F	39,8	9,5	4,74	Juv	1	16	27
17.09.2017	*P. auritus*	071	M	39,4	7,65	4,31	Ad	1	8	12
17.09.2017	*P. auritus*	257	M	39,0	7,95	5,16	Ad	0	12	20
24.09.2017	*M. daubentonii*	317	F	37,2	8,80	4,77	Juv	1+	11	16
26.09.2017	*P. auritus*	087	M	37,6	7,37	4,48	Ad	1	4	12
26.09.2017	*P. auritus*	125	F	39,2	6,90	4,78	Ad	1	3	12
15.10.2017	*P. auritus*	384	M	39,1	7,60	3,95	Juv	1	6	10
16.10.2017	*P. auritus*	268	F	39,6	8,32	4,93	Ad	1	0	20
16.10.2017	*P. auritus*	368	M	38,6	9,80	4,49	NA	2	21	21

Results

1. Hibernacula in abandoned human-made mines

1.1. The Sognsvann mine

The average bat count over the period of the surveys is 4.39 individuals (Table 2). The maximum numbers of bats that have been observed in the mine per survey round is 9 individuals (winter of 2018). The mean, minimum and maximum temperature inside the Sognsvann mine over the time of the surveys have been respectively: 2.547 ºC, - 6.5 ºC and 9 ºC. Overall, there has been a significant increase in maximum number of individuals recorded per year in the Sognsvann mine between 1987 and 2018 (generalized linear model: $z = 2.1$, $p = 0.036$) (Fig. 3 - 7). There has not been a significant change in temperature over the same period. As the temperature outside of the mine has increased, the inside temperature has also increased (generalized additive model: $R^2 = 0.70$, $t = 38.1$ $p<0.001$) (Fig. A1).

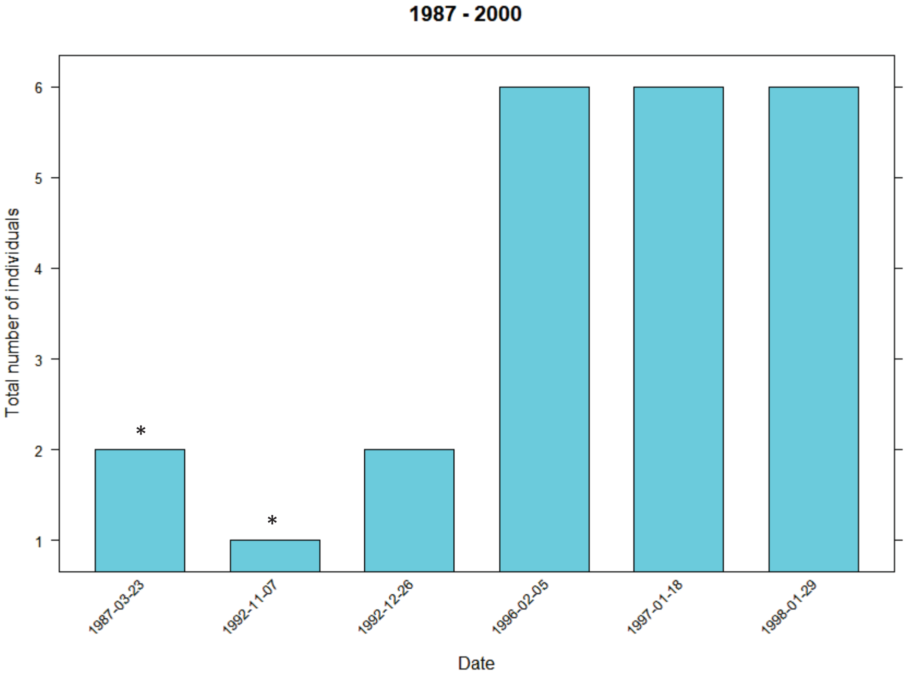

Figure 3. Total number of bat individuals counted for every survey in the mine at Sognsvann (1987-2000). The mine was surveyed six times in this period. * denote that the survey was carried out early/late (i.e. before late December or after February.

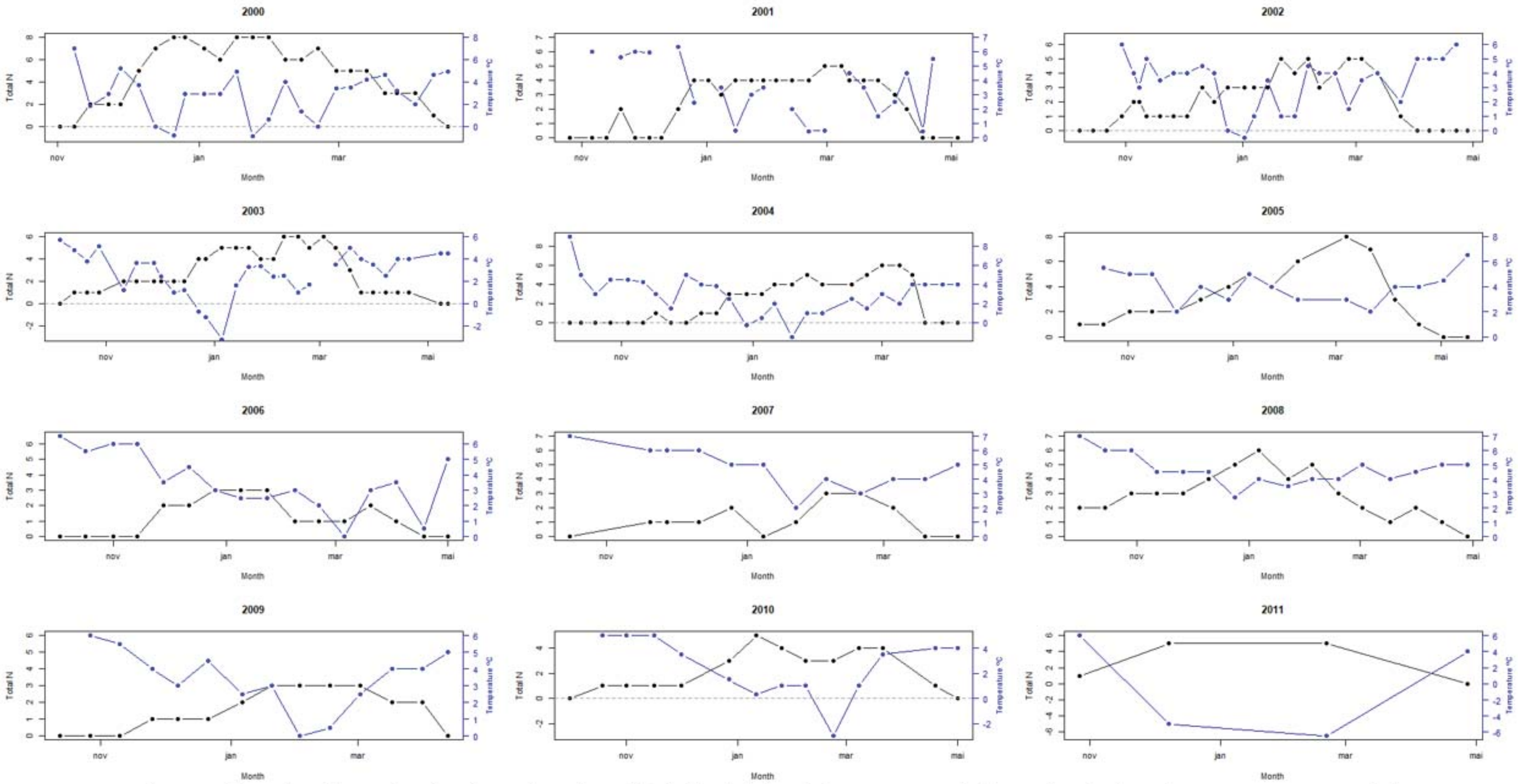

Figure 4. Plate of 12 figures showing the total number of individuals (N) and the temperature (°C) over time in the mine at Sognsvann recorded during every visit from year 1999 through 2011. Black line = Total number of individuals, blue line = Temperature inside the mine. Grey stapled line denotes zero. The year shown above each figure denotes which winter season the figure is showing (e.g. 2000: November 1999 – April 2000). Details about each year is found in table 4.

Table 4. Survey details from the Sognsvann mine (1999 – 2011).

Year	Information
2000	The first bat in the winter of 2000 was observed 15.11. The maximum number of individuals recorded that year was eight, and was observed in the period 21.12 – 31.01, with a drop to six and seven individuals in early January. No individuals were observed 17.04. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 2.25 ºC.
2001	The first two bats in the winter of 2001 were observed 20.11. The maximum number of individuals recorded that year was five, and was observed in the period 28.02. – 08.03. No individuals were observed 17.04. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 2.80 ºC.
2002	The first bat in the winter of 2002 was observed 30.10. The maximum number of individuals recorded that year was five, and was observed in the period 21.01. – 04.03, with a drop to four and three individuals during this period. No individuals were observed 02.04. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 3.01 ºC.
2003	The first bat in the winter of 2003 was observed 14.10. The maximum number of individuals recorded that year was six, and was observed in the period 09.02. – 03.03. No individuals were observed 08.05. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 2.00 ºC.
2004	The first bat in the winter of 2004 was observed 17.11. The maximum number of individuals recorded that year was six, and was observed in the period 01.03. – 09.03. No individuals were observed 21.03. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 2.22 ºC.
2005	There was already a bat in the mine during the first survey in the winter of 2005 (04.10.). The maximum number of individuals recorded that year was eight, and was observed during only one survey day (07.03.). No individuals were observed 02.05. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 3.55 ºC.
2006	The first two bats in the winter of 2006 was observed 28.11. The maximum number of individuals recorded that year was three, and was observed in the period 26.12. – 23.01. No individuals were observed 18.04. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 3.36 ºC.
2007	The first bat in the winter of 2007 was observed 20.11. The maximum number of individuals recorded that year was three, and was observed 04.02. – 19.02. No individuals were observed 19.03. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 4.44 ºC.
2008	There were already two bats in the mine during the first survey in the winter of 2008 (01.10.). The maximum number of individuals recorded that year was six, and was observed during only one survey day (06.01.). No individuals were observed 28.04. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 4.38 ºC.
2009	The first bat in the winter of 2009 was observed 25.11. The maximum number of individuals recorded that year was three, and was observed 20.01. – 02.03. No individuals were observed 12.04. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 2.80 ºC.
2010	The first bat in the winter of 2010 was observed 19.10. The maximum number of individuals recorded that year was five, and was observed during only one survey day (11.01.). No individuals were observed 01.05. or later that spring (Fig. 4). The mean temperature inside the mine this winter was 1.52 ºC.
2011	There was only four survey days during 2011, but there was observed five bats in the mine during the surveys Dec 8 and Feb 20. No individuals were observed 27.04. or later that spring (Fig. 4). The mean temperature inside the mine this winter was - 3.96 ºC (based on only 4 measurements).

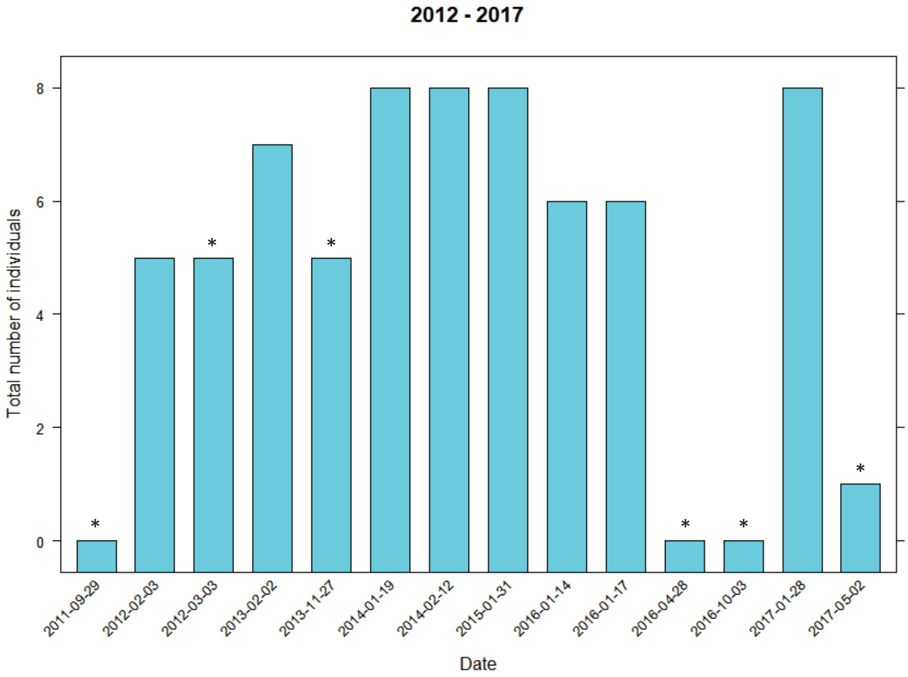

Figure 5. Total number of bat individuals counted for every survey in the mine at Sognsvann (2012-2017). The mine was surveyed 14 times in this period. * denote that the survey was carried out early/late (i.e. before late December or after February.

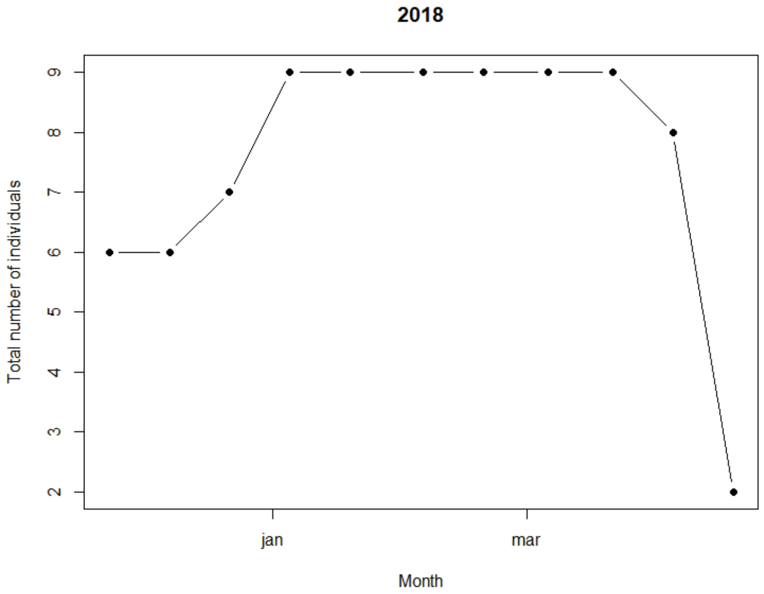

Figure 6. Total number of bat individuals counted for every survey in the mine at Sognsvann for the winter of 2017 – 2018. The mine was surveyed 11 times this winter (My observations).

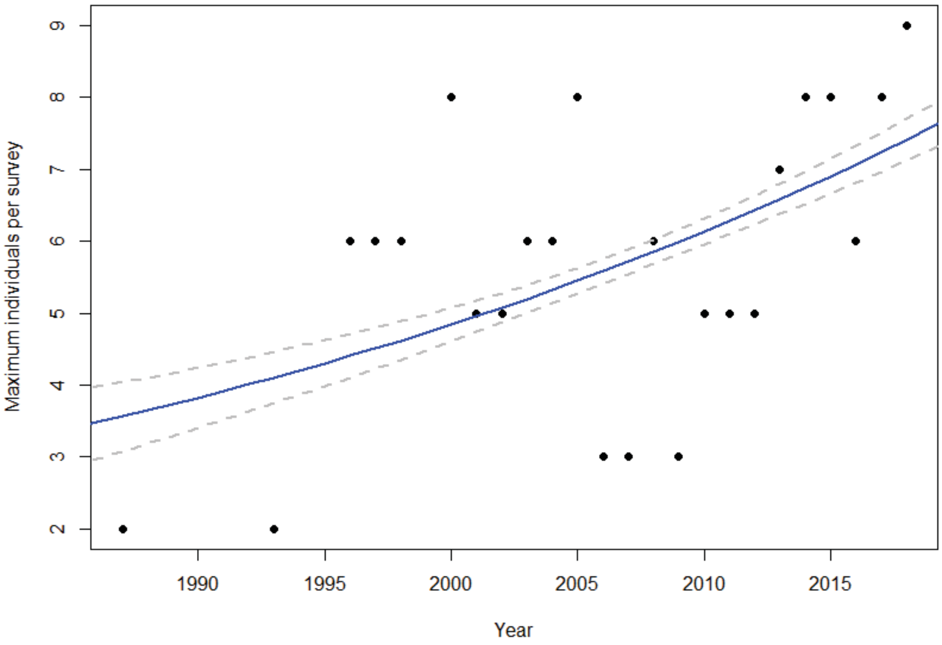

Figure 7. Estimated maximum number of bat individuals counted per year in the mine at Sognsvann (1987-2018). Blue line = line of best fit. Grey stapled lines = 95% confidence intervals.

The temperature differed throughout the mine. The logger located 40 meters inside the mine recorded the most stable temperatures (maximum difference: 4.25 ºC, Fig. 8, Table 5). The loggers at 10, 20, 30 and 60 meters all recorded negative temperatures, whilst the loggers at 40 and 50 meters never did (Fig. 8, Table 5). The temperature outside of the mine ranged from -15 to 13 ºC. The logger at 10 meters was the only logger that recorded humidity levels throughout the winter (%) (Fig. 9). The mean ± SD humidity at this point was 84.6 ± 6.46 % (Table 5).

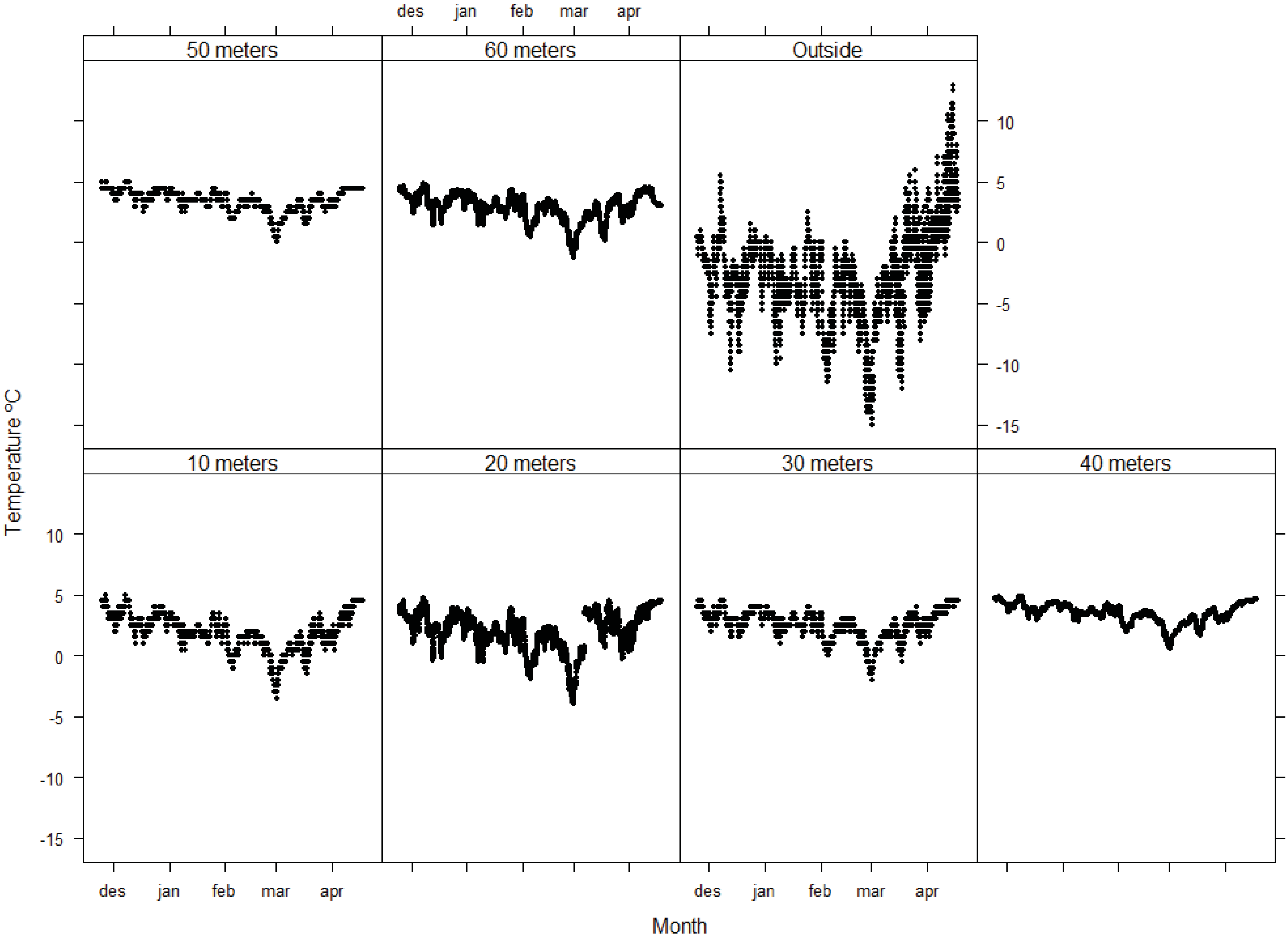

Figure 8. Temperature (ºC) at Sognsvann during the winter of 2017 – 2018 (late November – mid April) recorded with seven temperature loggers (one on the outside, and six inside the mine, at increasing distances from the mine entrance). Note that two different loggers were used, with different measurement precision.

Table 5. Temperature logger (temperature and humidity) details at Sognsvann mine, winter 2017 – 2018.

Location	Temperature ºC			
	Range (min-max)	Difference	Mean ± SD	Median
Outside	- 15 – 13	28	- 2.67 ± 3.78	- 2.5
10 meters	- 3.5 – 5	8.5	1.97 ± 1.5	2
20 meters	- 3.94 – 4.74	8.68	2.05 ± 1.58	2.2
30 meters	- 2 – 4.5	6.5	2.6 ± 1.18	2.5
40 meters	0.6 – 4.85	4.25	3.48 ± 0.81	3.53
50 meters	0 – 5	5	3.46 ± 0.89	3.5
60 meters	- 1.22 – 4.87	6.09	2.91 ± 1.08	3.07
	Humidity (%)			
10 meters	62.5 – 95.5	33	84.6 ± 6.46	85

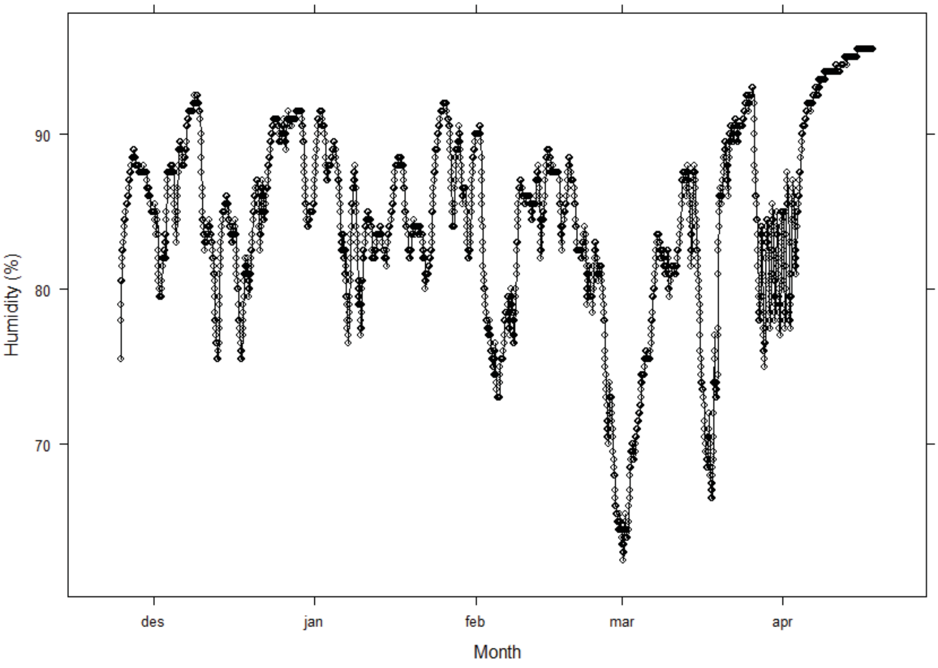

Figure 9. Humidity (%) levels from the logger at 10 meters from the entrance in the Sognsvann mine during the winter of 2017-2018 (late November – mid April).

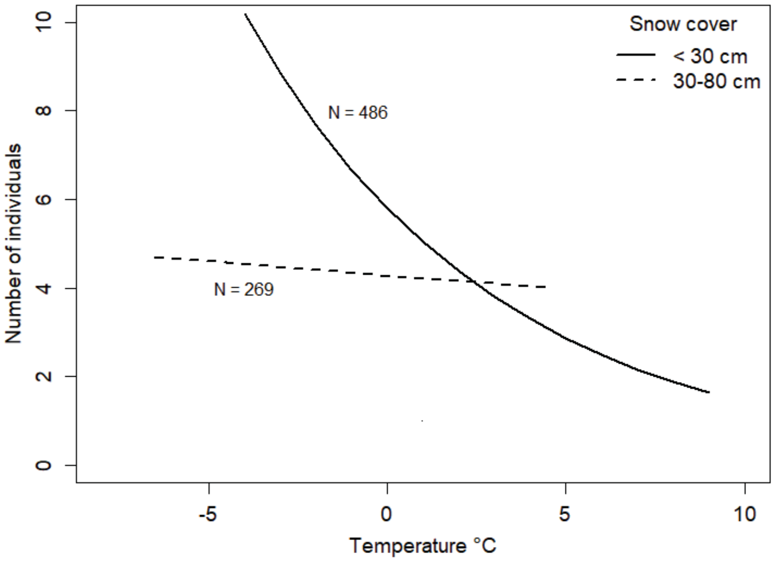

Figure 10. Interaction plot of temperature (inside the mine) and snow cover on number of individuals in the Sognsvann mine.

When the snow cover was shallow (<30 cm), there was a significant negative relationship between temperature and number of individuals in the mine at Sognsvann (Fig. 10, glm: z = -13.38, p<0.001). There was no difference between medium (30-60 cm) and deep (>60) snow cover, and thus they were combined. When the snow cover was >30 cm, there was no significant relationship between temperature and number of individuals (Fig. 10, glm: z = -1.061, p = 0.3).

There was a significant difference between northern bats and Daubenton's bats when comparing the bats' distances to the mine entrance (Fig. 11, Table 6). Daubenton's bats were found to be hibernating significantly deeper into the mine than northern bats. It should be noted that there was a large difference in sample size between the two species (Northern bats = 734, Daubenton's bats = 10). The mean distance to the entrance for northern bats was 27.3 meters (sd = 7), and the mean distance to the entrance for Daubenton's bats was 39.5 meters (sd = 5.6, median = 43.9, range: 31-43.9). The northern bats have been observed hibernating solitarily 489 times, and in a group (two – six individuals) 197 times. The ten registered Daubenton's bats have all been observed hibernating solitarily (there was only one Daubenton's bat at a time in the mine).

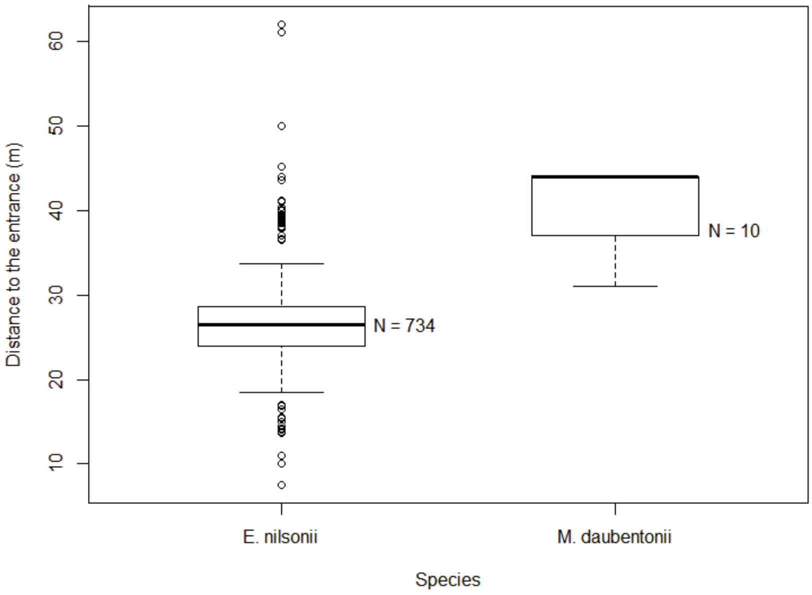

Figure 11. Distribution of bat species in the mine at Sognsvann. Relationship between species and distance to the entrance (meters). N = total number of bat observations.

Table 6. Pairwise comparison test between species on the distance to the entrance (meters) in the mine at Sognsvann.

Comparisons	Difference (value)	p
M. daubentonii – E. nilsonii	12.22	<0.001

1.2. Analysis of the mines at Alnsjøen, Djupdal, Engelstadtjern, Engelstadvang, Røysåsen and Spenningsby

There has been a significant increase in the total number of individuals in the mines at Djupdal (linear regression: t = 3.03, p = 0.006), Røysåsen (linear regression: t = 9.7, p<0.001), and Engelstadtjern (linear regression: t = 4.5, p>0.001) over the time of the surveys (Fig. 12). Figure 13 also shows that the mine at Spenningsby had a slight increase (linear regression: t = 2.02, p=0.045), whereas the two other mines (Alnsjø and Engelstadvang) have not had any significant changes in total number of individuals over the period of the surveys (Alnsjø; linear regression: t = - 1.5, p = 0.13, Engelstadvang; linear regression: t = 1.2, p = 0.24).

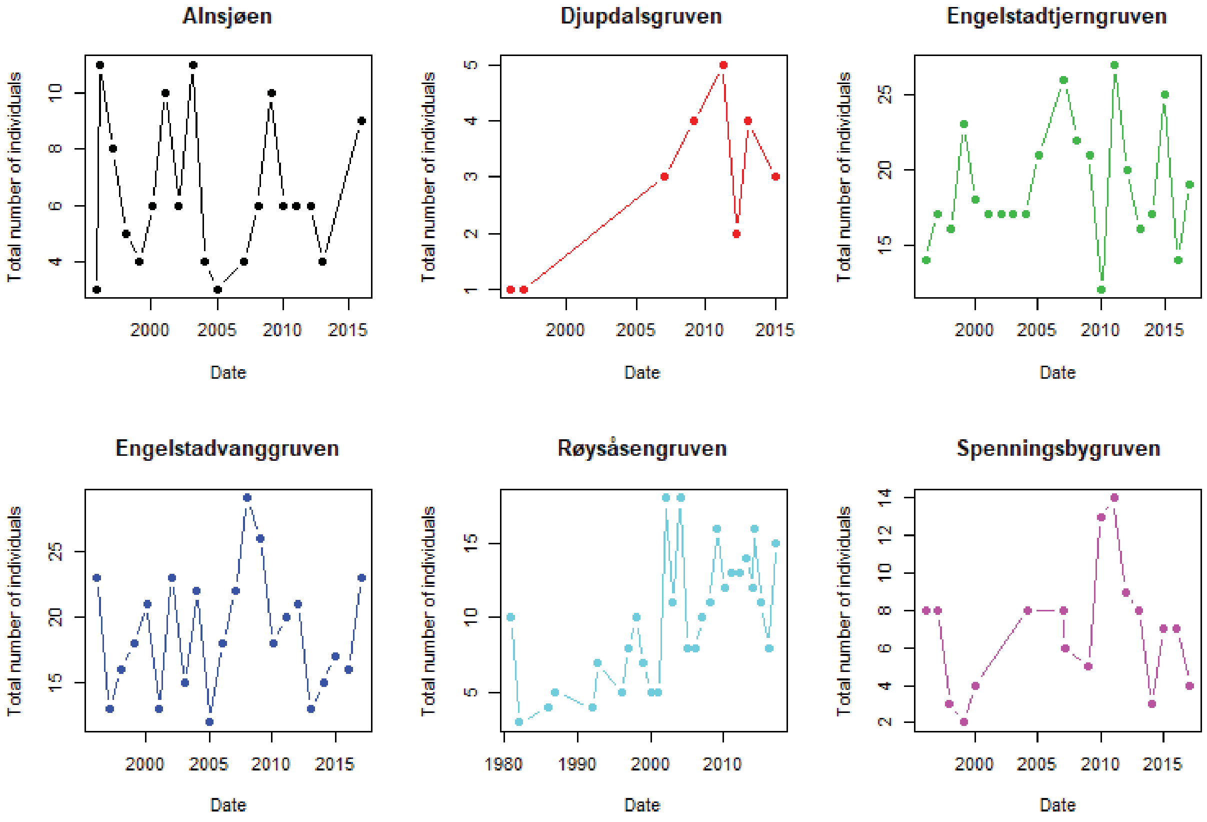

Figure 12. Total number of individuals counted in the mines at Alnsjøen, Djupdal, Engelstadtjern, Engelstadvang, Røysåsen and Spenningsby per survey (1981-2017). Each mine was surveyed 1-2 times per hibernation season (December-February). Note that the y-axes have different lengths.

Mine identity had a significant effect on the relationship between temperature and snow depth in the mines (Chi square test: $\chi^2 = 20.646$, df = 15, p<0.001).

At Alnsjøen, there was a significant negative relationship between number of individuals and temperature when the snow cover was shallow (< 30 cm) (Fig. 13, glm: z = -3.463, p<0.001), but no significant relationship at medium and deep snow cover (> 30 cm, medium and deep were combined due to low number of deep snow cover measurements).

At Djupdalen, there were no significant relationships between number of individuals and temperature in any of the snow cover intervals (Fig. 13, shallow glm: z = -0.667, p = 0.505, medium glm: z = 1.838, p = 0.066, deep glm: z = 0.697, p = 0.486). Note that the sample size was small for this mine: N (shallow) = 8, N (medium) = 6, N (deep) = 9.

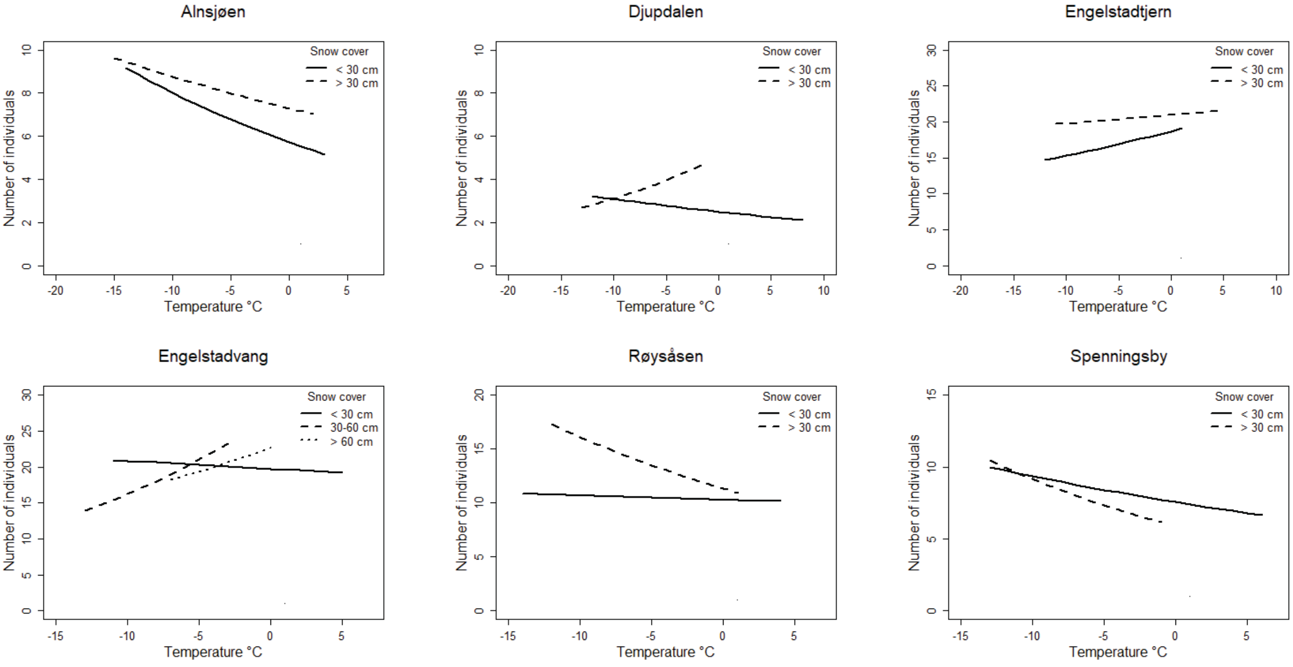

Figure 13. Interaction plot of temperature (°C) and snow cover (cm) on number of individuals in all mines (excluding Sognsvann). Full line denotes snow cover < 30 cm, stapled line denotes snow cover > 30 cm (except for Engelstadvang: stapled line denotes 30-60 cm and dotted line denotes > 60 cm). Note that the x- and y-axes have different lengths.

At Engelstadtjern, there was a significant positive relationship between number of individuals and temperature during shallow snow cover (< 30 cm) (Fig. 13, glm: z = 2.97, p = 0.003), but no significant relationships during medium (glm: z = 1.828, p = 0.0675) or deep (glm: z = 1.90, p = 0.0575) snow cover.

At Engelstadvang, there was no significant relationship between number of individuals and temperature during shallow snow cover (< 30 cm) (Fig. 13 glm: z = -1.33, p = 0.184), but there were significant positive relationships during medium (30-60 cm) (glm: z = 8.816, p<0.001) and deep (> 60 cm) (glm: z = 3.622, p<0.001) snow cover intervals.

At Røysåsen, there was no significant relationship between number of individuals and temperature during shallow snow cover (< 30 cm) (Fig. 13, glm z = -0.746, p = 0.456), but there was a significant negative relationship during medium and deep snow cover (> 30 cm, medium and deep were combined due to low number of deep snow cover measurements) (glm: z = -4.192, p<0.001).

At Spenningsby, there were significant negative relationships between number of individuals and temperature during both shallow (< 30 cm, glm: z = -2.427, p = 0.0152) and medium/deep (> 30 cm, glm: z = -3.293, p<0.001) snow cover intervals (Fig. 13). Medium and deep were combined due to low number of deep snow cover measurements (N = 8).

Most bats were found less than 200 meters from the nearest mine entrance (Fig. 14 and 15, Table 7). See Table 2 for mine configurations. In the Alnsjøen mine, bats were observed throughout the entire mine, with observations ranging from 6 to 651 meters. 57.4 % of the registrations were Daubenton's bats (Table 7). In the Djupdal mine, the bats' mean distance to the entrance was 35.9 meters, and 78.3% of the registrations were brown long eared bats (Table 7). There were no observations of whiskered/Brandt's bats in this mine. In the mine at Engelstadtjern, the bats were observed between 1 and 194 meters, and the proportion of species was relatively evenly distributed (18.6 – 34%), with northern bats being the least numerous and whiskered/Brandt's bats the most numerous species (Table 7).

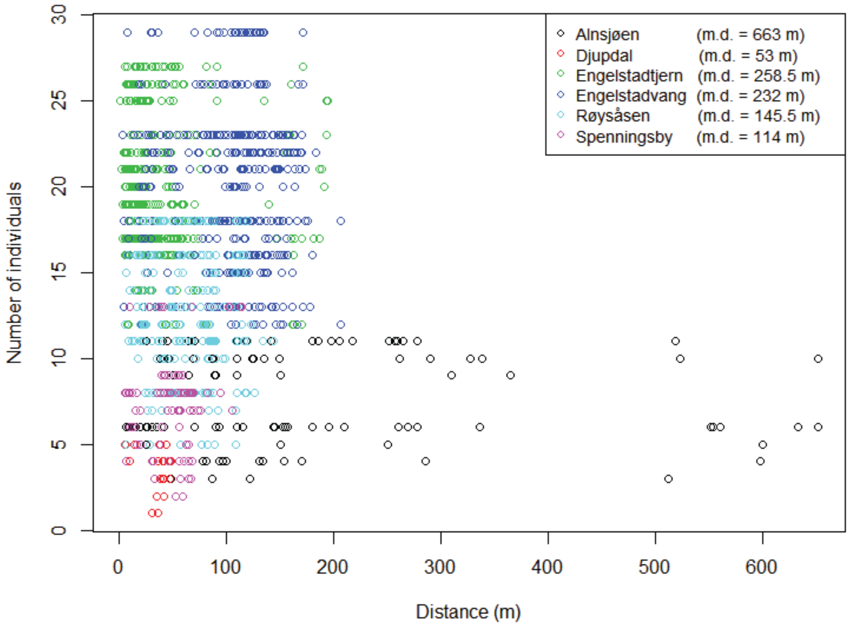

Figure 14. Relationship between distance (m) to nearest entrance and the total number of individuals in all mines (excluding Sognsvann). m.d. = Max distance from entrance(s) to the furthest point away from the entrance(s).

In the mine at Engelstadvang, the bats were observed between 3 and 206 meters from the entrance, and the most numerous group of bats were whiskered/Brandt's bats (43% of the observations, Table 7). In the mine at Røysåsen, the bats' mean distance to entrance was 61.7 meters, and the most numerous bats were whiskered/Brandt's bats (35.1%) and Daubenton's bats (29.4%) (Table 7). In the mine at Spenningsby, the bats' mean distance to entrance was 50 meters, and the most numerous species was brown long eared bats (40% of the observations) (Table 7).

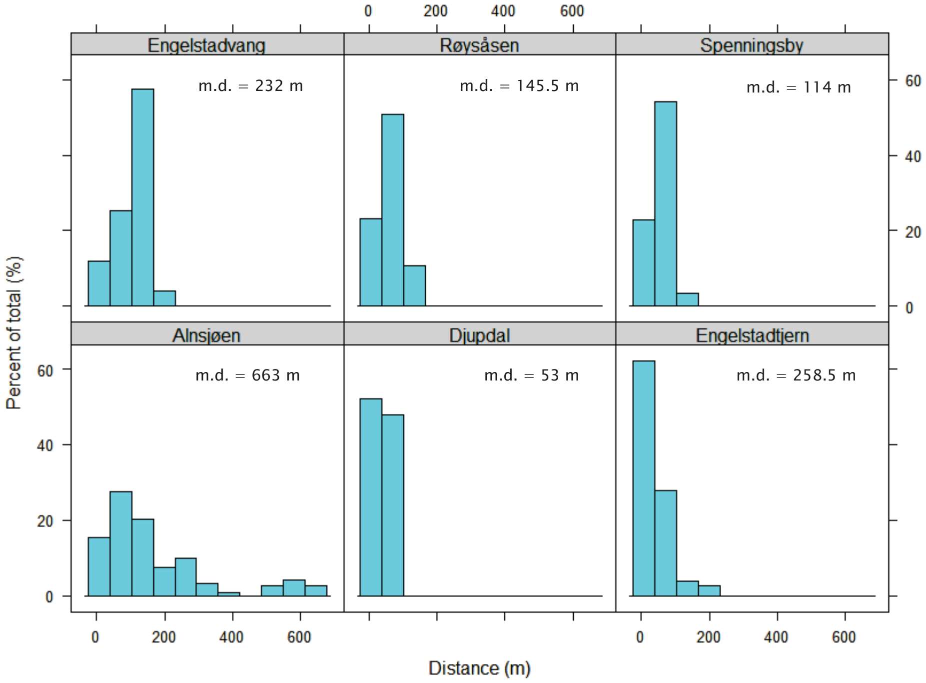

Figure 15. Histogram of the distribution of bats relative to the mine entrance during all surveys in the mines. m.d. = Max distance from entrance(s) to the furthest point away from the entrance(s).

Table 7. Distribution details of the bats: range, mean ± SD, median, max depth (meters) (Max distance from entrance(s) to the furthest point away from the entrance(s)), and species percentages (%).

Mine	Distribution characteristics (meters from mine entrance)			
	Range (min – max)	Mean ± SD	Median	Max depth (m)
Alnsjøen	6 – 651	165 ± 160.7	110	663
Djupdal	5 – 48.5	35.9 ± 11.74	38.5	53
Engelstadtjern	1 – 194	39.15 ± 39.57	25.5	258.5
Engelstadvang	3 – 206	105.9 ± 42.6	113	232
Røysåsen	5 – 144	61.7 ± 31.2	61	145.5
Spenningsby	5 – 114	50 ± 24.9	55	114
	Species percentages % (number of individuals)			
	Brown long eared bats	Northern bats	Whiskered/Brandt's bats	Daubenton's bats
Alnsjøen	9.8 % (12)	7.4 % (9)	25.4 % (31)	57.4 % (70)
Djupdal	78.3 % (18)	13 % (3)	0	8.7 % (2)
Engelstadtjern	25 % (102)	18.6 % (76)	34 % (139)	22.5 % (92)
Engelstadvang	28.6 % (118)	11.4 % (47)	43 % (177)	17 % (70)
Røysåsen	18.44 % (52)	17 % (48)	35.1 % (99)	29.4 % (83)
Spenningsby	40 % (46)	23.5 % (27)	15.65 % (18)	20.87 % (24)

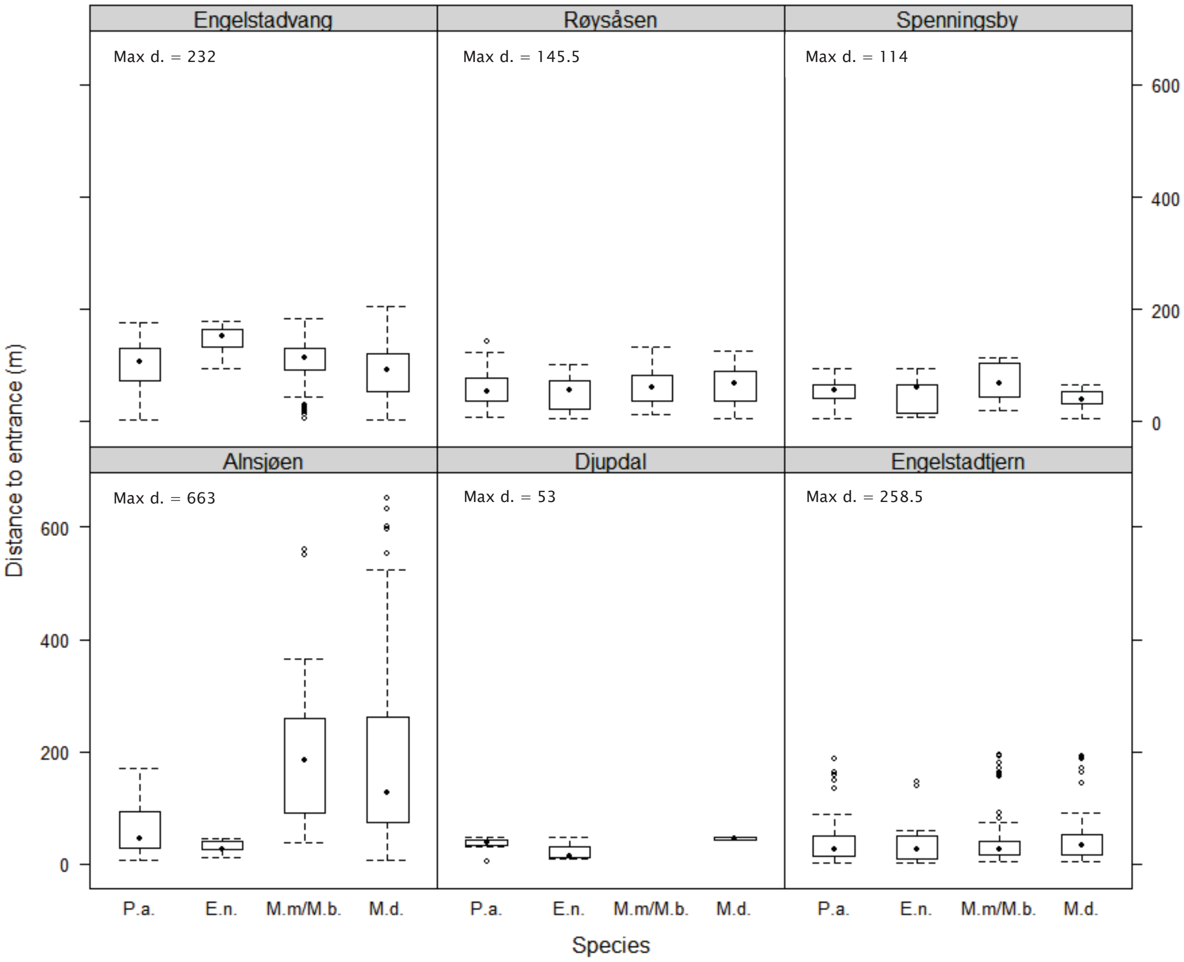

Figure 16. Distribution of bat species. Box plots of distances to the nearest mine entrance (m) for P.a. = *P. auritus*, E.n. = *E. nilsonii*, M.m/M.b. = *M. mystacinus/Brandtii* and M.d. = *M. daubentonii* in all mines (excluding Sognsvann). Max d. = Max distance from entrance(s) to the furthest point away from the entrance(s).

Mine identity had a significant effect on the distribution of bats (distance to entrance) in the mines (Chi square test: $\chi^2 = 135.24$, df = 14, $p<0.001$).

Table 8. Pairwise comparisons test between species with respect to distance to the nearest mine entrance (m) in the Alnsjøen mine.

Comparisons	Difference (value)	t	p
E. nilsonii – P. auritus	-34.97	-0.520	0.6
M. mystacinus/brandtii – P. auritus	133.22	2.543	0.0124
M. daubentonii – P. auritus	127.46	2.654	0.009
M. mystacinus/brandtii – E. nilsonii	168.19	2.89	0.005
M. daubentonii – E. nilsonii	162.431	2.99	0.003
M. daubentonii - M. mystacinus/brandtii	5.763	0.169	0.87

At Alnsjøen, the whiskered/Brandt's bats hibernated significantly further into the mine than the brown long eared bats and the northern bats, and the Daubenton's bats hibernated significantly further into the mine than the brown long eared bats and the northern bats. There were no other significant differences (Fig. 16, Table 8).

Table 9. Pairwise comparisons test between species with respect to distance to the nearest mine entrance (m) in the Djupdalen mine.

Comparisons	Difference (value)	t	p
E. nilsonii – P. auritus	-13.5	-2.00	0.0591
M. daubentonii – P. auritus	9.167	1.137	0.27
M. daubentonii – E. nilsonii	22.67	2.296	0.0326

At Djupdalen, the Daubenton's bats hibernated significantly further into the mine than the northern bats. There were no significant differences in the other comparisons (Fig. 17, Table 9).

At Engelstadtjern, there were no significant differences in distance to the nearest entrance between the species (Fig. 16, Table 10).

At Engelstadvang, the northern bats hibernated significantly further into the mine than the brown long eared bats, the Daubenton's bats and the whiskered/Brandt's bats. The whiskered/Brandt's bats hibernated significantly further into the mine than the Daubenton's bats (Fig. 16, Table 11).

Table 10. Pairwise comparisons test between species with respect to distance to the nearest mine entrance (m) in the Engelstadtjern mine.

Comparisons	Difference (value)	t	p
E. nilsonii – P. auritus	-5.267	-0.88	0.38
M. mystacinus/brandtii – P. auritus	5.544	1.077	0.28
M. daubentonii – P. auritus	6.482	1.132	0.26
M. mystacinus/brandtii – E. nilsonii	10.811	1.891	0.0594
M. daubentonii – E. nilsonii	11.75	1.882	0.06
M. daubentonii - M. mystacinus/brandtii	0.938	0.173	0.86

Table 11. Pairwise comparisons test between species with respect to distance to the nearest mine entrance (m) in the Engelstadvang mine.

Comparisons	Difference (value)	t	p
E. nilsonii – P. auritus	49.750	7.241	<0.001
M. mystacinus/brandtii – P. auritus	8.169	1.717	0.087
M. daubentonii – P. auritus	6.521	1.084	0.28
M. mystacinus/brandtii – E. nilsonii	-41.580	-6.369	<0.001
M. daubentonii – E. nilsonii	-56.270	-7.509	<0.001
M. daubentonii - M. mystacinus/brandtii	-14.69	-2.614	0.009

Table 12. Pairwise comparisons test between species with respect to distance to the nearest mine entrance (m) in the Røysåsen mine.

Comparisons	Difference (value)	t	p
E. nilsonii – P. auritus	-6.741	-0.863	0.389
M. mystacinus/brandtii – P. auritus	3.643	0.636	0.525
M. daubentonii – P. auritus	7.193	1.229	0.22
M. mystacinus/brandtii – E. nilsonii	10.384	1.475	0.14
M. daubentonii – E. nilsonii	13.933	1.95	0.052
M. daubentonii - M. mystacinus/brandtii	3.549	0.743	0.458

At Røysåsen, there were no significant differences in distance to the nearest entrance between the species, but the difference between Daubenton's bats and northern bats was almost significant (Daubenton's bats further in than northern bats) (Fig. 16, Table 12).

At Spenningsby, the whiskered/Brandt's bats hibernated significantly further into the mine than the brown long eared bats, the northern bats, and the Daubenton's bats (Fig. 16, Table 13).

Table 13. Pairwise comparisons test between species with respect to distance to the nearest mine entrance (m) in the Spenningsby mine.

Comparisons	Difference (value)	t	p
E. nilsonii – P. auritus	-0.557	-0.09	0.93
M. mystacinus/brandtii – P. auritus	23.99	3.02	0.003
M. daubentonii – P. auritus	10.222	1.623	0.108
M. mystacinus/brandtii – E. nilsonii	24.545	2.857	0.005
M. daubentonii – E. nilsonii	-9.665	-1.362	0.18
M. daubentonii - M. mystacinus/brandtii	-34.21	-3.951	<0.001

2. Roosts and activity in the autumn season in the core study area

2.1. Radio telemetry

We radio-tagged 15 individuals in total; 12 brown long eared bats, two Daubentons's bats, and one northern bat (Table 4). These individuals led us to find 11 different roost sites (Table 14). The tagged individuals used three different buildings (two houses, one cabin annex), two barns, three trees (birch trees, one of which was deceased), two rock face crevices, and one abandoned mine (Spenningsby) (Table 14). Four of the used radio tags were relocated after falling off the bats, two bats were never relocated after release, and nine radio transmitters were lost or ran out of battery after successfully leading us to locate at least one roost site per individual.

Table 14. Individual ID, species, sex (M=male, F=female), tracking period and roost type selection of the bats radio-tagged in the field period. (*) Spent the given number of days in the same roost. (**) Individual was not prioritized, due to inactivity over a prolonged period. NR = Individual was not relocated. RAT = Relocated by airplane tracking after it had lost its transmitter.

				Number of days in roost type						
Individual	Species	Sex	First-last record	Building	Crevice	Tree	Barn	Mine	Unknown	Comments
395	*P. auritus*	M	23.08-29.08.	1	2	1	1	1	0	Transmitter lost
106	*P. auritus*	M	23.08-03.09.	6 *	0	4 *	0	0	0	Empty battery **
281	*M. daubentonii*	F	23.08-30.08.	0	0	0	0	0	NR	Never relocated
285	*E. nilsonii*	M	28.08-12.09.	3 *	0	0	11 *	0	0	Empty battery
342	*P. auritus*	F	28.08-03.09.	0	0	0	3 *	0	0	Transmitter relocated
147	*P. auritus*	M	12.09-15.09.	0	0	0	1	0	1	Transmitter relocated
331	*P. auritus*	F	12.09-30.09.	0	0	0	16 *	0	0	Signal lost
071	*P. auritus*	M	17.09-25.09.	0	0	0	1	0	0	Transmitter relocated
257	*P. auritus*	M	17.09-29.09.	0	0	0	0	0	RAT	Transmitter lost
317	*M. daubentonii*	F	24.09-05.10.	0	0	1	0	0	2+	Empty battery
087	*P. auritus*	M	26.09-30.09.	0	0	0	4 *	0	0	Signal lost
125	*P. auritus*	F	26.09-29.09-	0	0	0	3	0	0	Transmitter relocated
384	*P. auritus*	M	15.10-21.10.	0	0	0	6 *	0	0	Signal lost
268	*P. auritus*	F	16.10-17.10.	0	0	0	0	0	NR	Never relocated
368	*P. auritus*	M	16.10-06.11.	1	0	0	0	1	0	Last seen in mine

The barn at Nordre Berg (605094, 6662048) was used as a day roosting site by eight different tagged individuals (seven *P. auritus* and one *E. nilsonii*) (Table 14, Plate 2). We observed brown long eared bats in flight inside of the main room and in the barn cellar at night on several occasions, and we also observed northern bats hunting above and around the barn.

Brown long eared bats

The brown long eared bat #395 (male) changed roosts every night, and moved between six different locations (Table 14). This individual was captured and tagged outside of the Spenningsby mine, and utilized the annex of a cabin (Ramdalskollen), a birch tree in a swamp, the barn at Nordre Berg, two different rock face crevices, and the mine itself as roost sites (plate 2). This individual was observed hunting in the mixed forest area surrounding Bergstjern (Fig. 17). The transmitter was located in a spruce tree approximately 50 meters north of the original capture site. The transmitter stayed in this tree for a week (transmitter lost).

The brown long eared bat #106 (male) changed roosts between a white wooden house (large hole in both the north and south wall of the building) and a birch tree in Gjerdrum (Table 14, plate 3). This individual was also captured and tagged outside of the Spenningsby mine, and we observed its hunting area to stretch between the two roosts, northeast of Bergstjern (Fig. 17).

The brown long eared bat #342 (female) was captured at the barn (Nordre Berg), and roosted there for three days (plate 2). The transmitter was found at the foot of a pine tree (3.2 km east of the barn). I observed one bat leaving that pine tree the night before we found the transmitter, but the radio transmitter stayed in the same location.

The brown long eared bat #147 (male) was captured at the barn (Nordre Berg), and roosted there the first day. The second day, it roosted at an unknown location, presumably west of the main road (Table 14, plate 2). On the third day, it had returned to the same barn. However, the signal remained stationary until the transmitter was relocated (a number of days later) on the floor inside the main room at the barn.

The brown long eared bat #331 (female) was captured at the barn (Nordre Berg), and spent 16 days roosting in this location (Table 14, plate 2). This individual spent most of its time hunting in the mixed forest northeast of the barn, but was also observed west of “Linfåningshøgda” (a 325 m a.s.l. hill 2 km southwest of the barn) and north of Bergstjern (Fig. 17). Her signal was lost the same day as we lost the signal of the brown long eared bat #087, 30.09.17.

The brown long eared bat #071 (male) was captured at the scree (Holterkollen). He was located several days after capture, during a random car search, roosting in a horse barn in Gjerdrum, 6.2 kilometers east of the capture site (Table 14, plate 3). I observed at least three brown long eared bats in flight inside of the barn loft where #071 roosted. The transmitter was relocated in a spruce tree 1.5 kilometers northwest of the horse barn (five meters above the ground) the following day.

The brown long eared bat #257 (male) was also captured at the scree (Holterkollen). The signal was found in Sørum municipality approximately 20 kilometers east of the capture site during airplane radio tracking 11 days after capture, but the transmitter was lost in a mixed forest. The signal remained unchanged the following days, and it is likely that the radio tag had fallen off.

Plate 2. (1) Nordre Berg barn, day roost of 7 *P. auritus* (395, 342, 331, 071, 087, 125 & 384) and 1 *E. nilsonii* (285) (Photo: Kristian F. Kristiansen). (2) Day roost of *E. nilsonii* (285) in annex next to the barn (Photo: Rune Sørås). (3) Day roost of *M. daubentonii* (317) in a dead birch (Photo: Rune Sørås). (4) Day roost of *P. auritus* (395) in a rock face crevice in the middle of a clear cut (Photo: Rune Sørås).

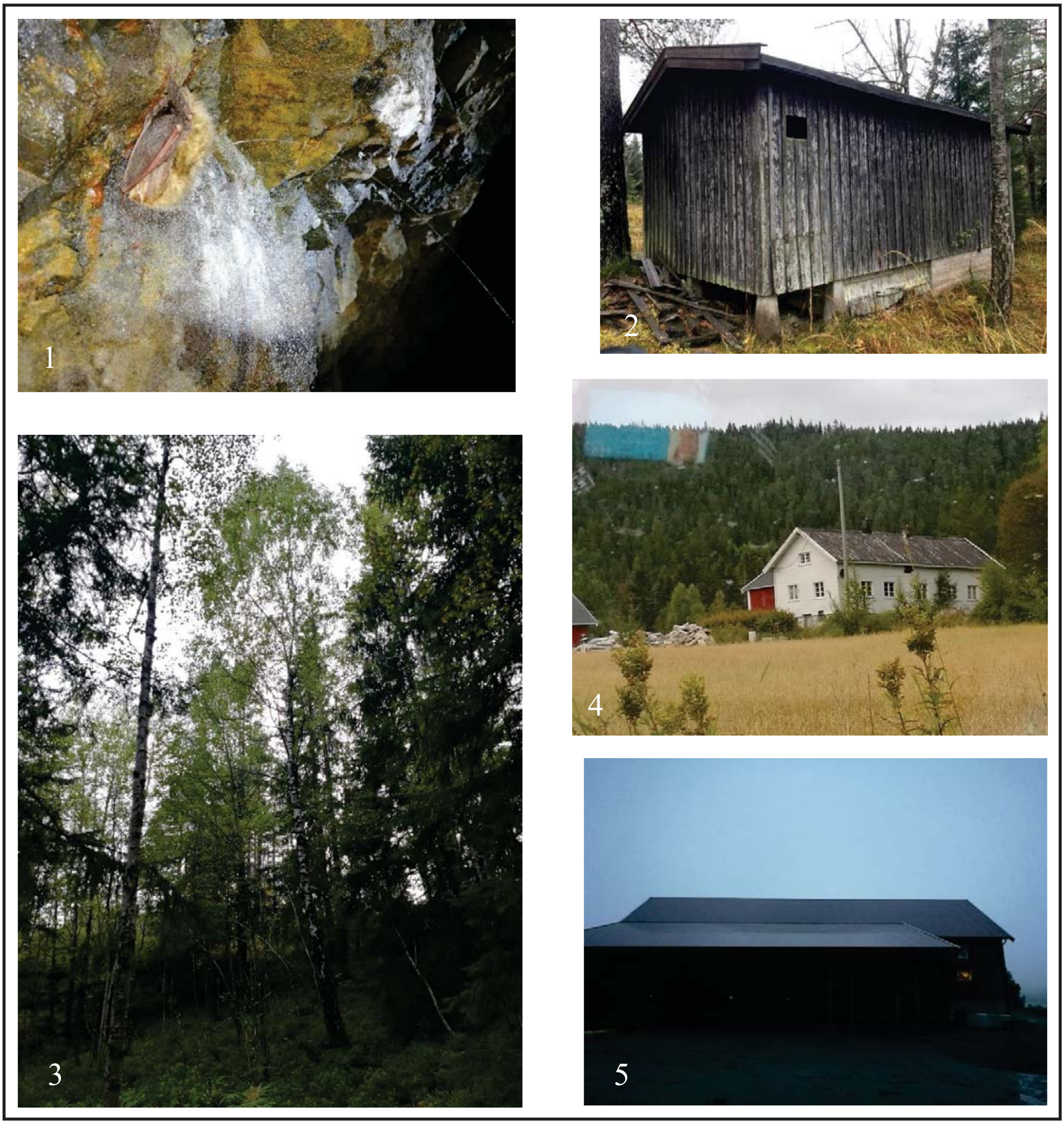

Plate 3. (1) Day roost of *P. auritus* (368) in the Spenningsby mine (Photo: Rune Sørås). (2) Day roost of 2 *P. auritus* (395 & 368) in a cabin annex (Photo: Kristian F. Kristiansen). (3) Day roost of *P. auritus* (106) in a birch tree (Photo: Rune Sørås). (4) Day roost of *P. auritus* (106) in a wooden house (Photo: Rune Sørås). (5) Day roost of P. auritus (071) in a horse barn (stable) (Photo: Kristian F. Kristiansen).

The brown long eared bat #087 (male) was captured at the barn (Nordre Berg), and stayed in this location for four days (Table 14, plate 2). The signal was then lost, the same day as #331, 30.09.17. We had no observations of this individual neither leaving the barn nor hunting outside of the barn.

The brown long eared bat #125 (female) was captured at the barn (Nordre Berg), and roosted in this location for three days (Table 14, plate 2). This individual was observed hunting in the forest southeast of Bergstjern (Fig. 17). Her transmitter was relocated several days after capture, hanging in a pine tree approximately 1.8 kilometers east of the capture site.

The brown long eared bat #384 (male) was captured using a harp trap at the barn (Nordre Berg), and roosted in this location for 6 days (Table 14, plate 2). We had visual observations and very strong signals of this individual on several occasions inside the main room of the barn the days after we radio tagged him. The signal of this bat was lost on the 21.10.17; he foraged for 20-30 minutes just east of the barn before suddenly taking off and disappearing.

The brown long eared bat #368 (male) was captured at the Spenningsby mine. He was observed hunting south of the mine. This individual was located roosting in a cabin annex approximately 500 meters southwest of his capture site (at Ramdalskollen, same as #395), and in the mine where he was captured (Table 14, plate 3). #368 was the last radio tagged individual of the field period. This individual was last observed roosting inside the mine where he was captured. During a January survey of this mine, this individual was not observed.

The brown long eared bat #268 (female) was never relocated after radio tagging and release. This individual was captured using a harp trap in the barn and fed with 27 meal worms.

Northern bat

The northern bat #285 (male) was captured at the barn (Nordre Berg). This bat stayed 11 days in the barn and three days in a small annex building 15 meters east of the barn (Table 14, plate 2). This individual was observed hunting around and above the barn, southeast of the Bergstjern lake, as well as in the forest area west of the barn, in the area around Nitelva river and above the main road going through Nittedal (Riksvei 4) (Fig. 18).

Daubenton's bats

The Daubenton's bat #317 (female) was captured at Li bridge (mist net set up under the bridge). This individual was observed hunting above the river surface north and south of the bridge. She was located roosting in a dead birch tree, 1.1 kilometers north of the bridge (Fig. 19, Table 14, plate 2). We have reason to be believe that this individual utilized at least two additional day roosts (observed moving southbound and northbound when an observer was located at the one known roost site, during the time of the evening when we expected the bat to emerge from the day roost). Another Daubenton's bat (#281, female) was never relocated after radio tagging and release.

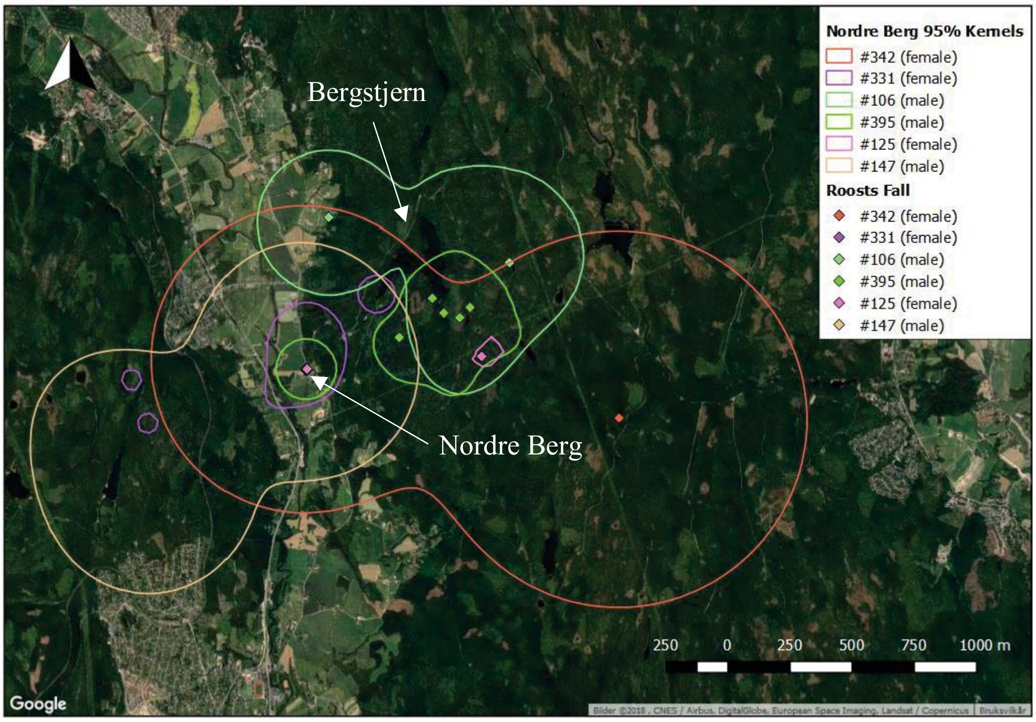

Figure 17. 95% Kernels of six brown long eared bats and their day roosts during the field period. Kernels are based on on-site plots, strong signal plots and triangulation plots. Note that the kernels for #125, #147 and #342 are based on a low number of observations.

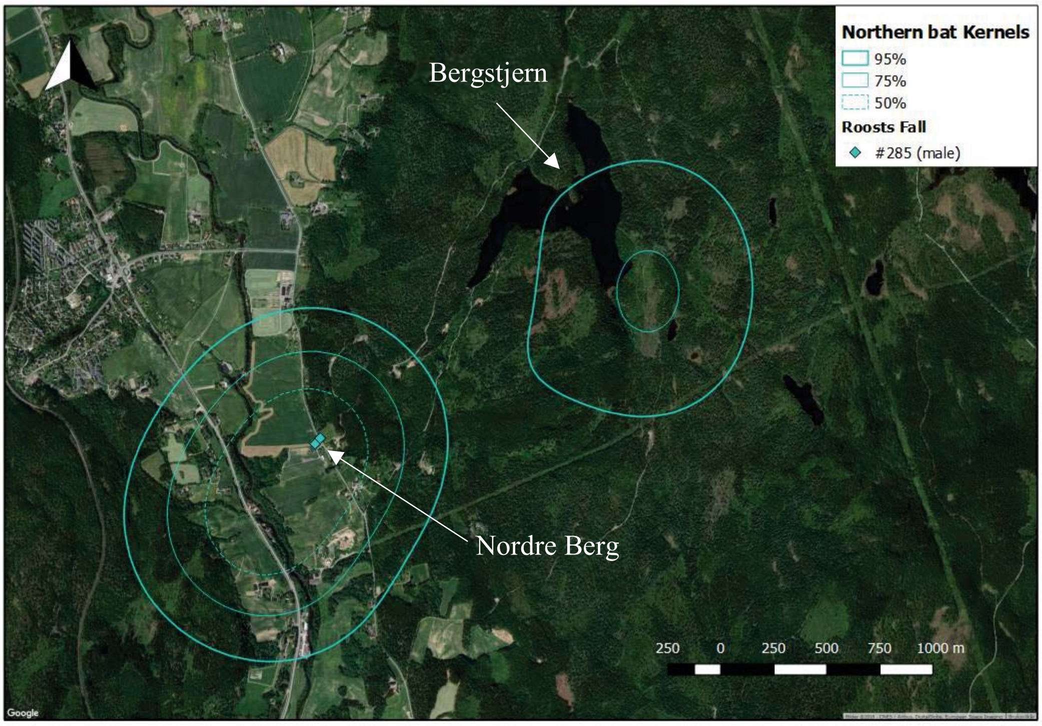

Figure 18. 95, 75 & 50% Kernel of #285, the northern bat roosting at the barn at Nordre Berg. Kernels are based on on-site plots, strong signal plots and triangulation plots.

Fig. 19. Map showing day roost (dead birch tree) and capture site of the female Daubenton's bat #317. Red circle = capture site (Li bridge).

2.2. Batlogger data (echolocation calls)

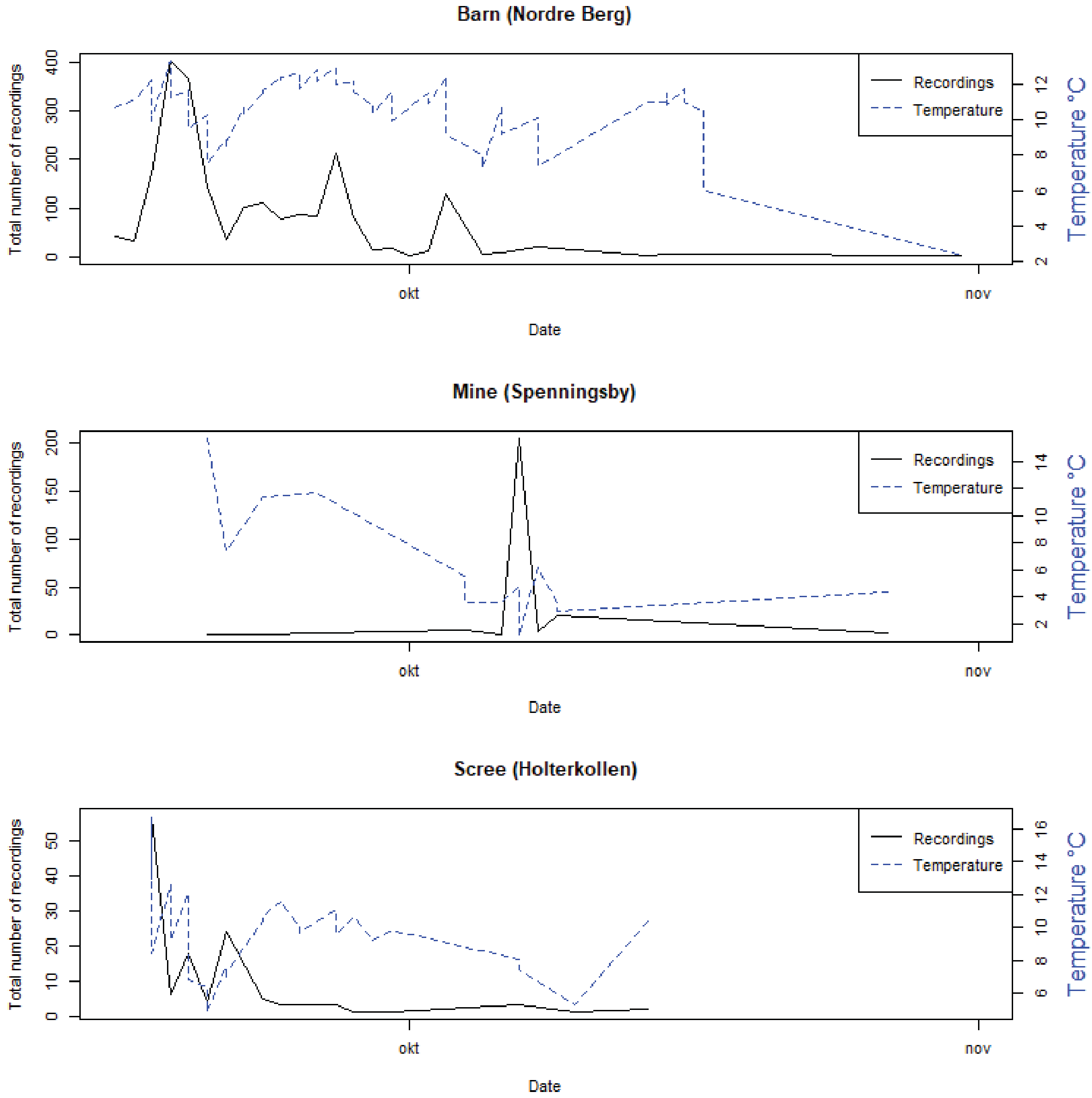

Figure 20. Total number of bat echolocation call recordings per night and temperature (ºC) at the different sites during the autumn period. Note that the axes have different lengths.

Plate 3. (1) Batlogger setup at the scree (Holterkollen) (Photo: Kristian F. Kristiansen). (2) Batlogger setup at Nordre Berg barn (Photo: Kristian F. Kristiansen). (3) Batlogger setup at the mine (Spenningsby) (Photo: Kristian F. Kristiansen).

The activity at the barn decreased significantly over the deployment period (Figures 21-22, glm: t = - 30.05, p<0.001). The maximum number of recordings at the barn was 403, and was recorded the night of 18. - 19.09.17.

There was not much activity at the mine (Spenningsby), with one notable exception on the night of 07. - 08.10.17, when a total number of 204 recordings were logged (Figures 21-22).

The activity at the scree also decreased significantly over the deployment period (Figures 21-22, glm: t = - 9.826, p<0.001). The maximum number of recordings at the scree was 57, and was recorded the night of 17. – 18.09.17.

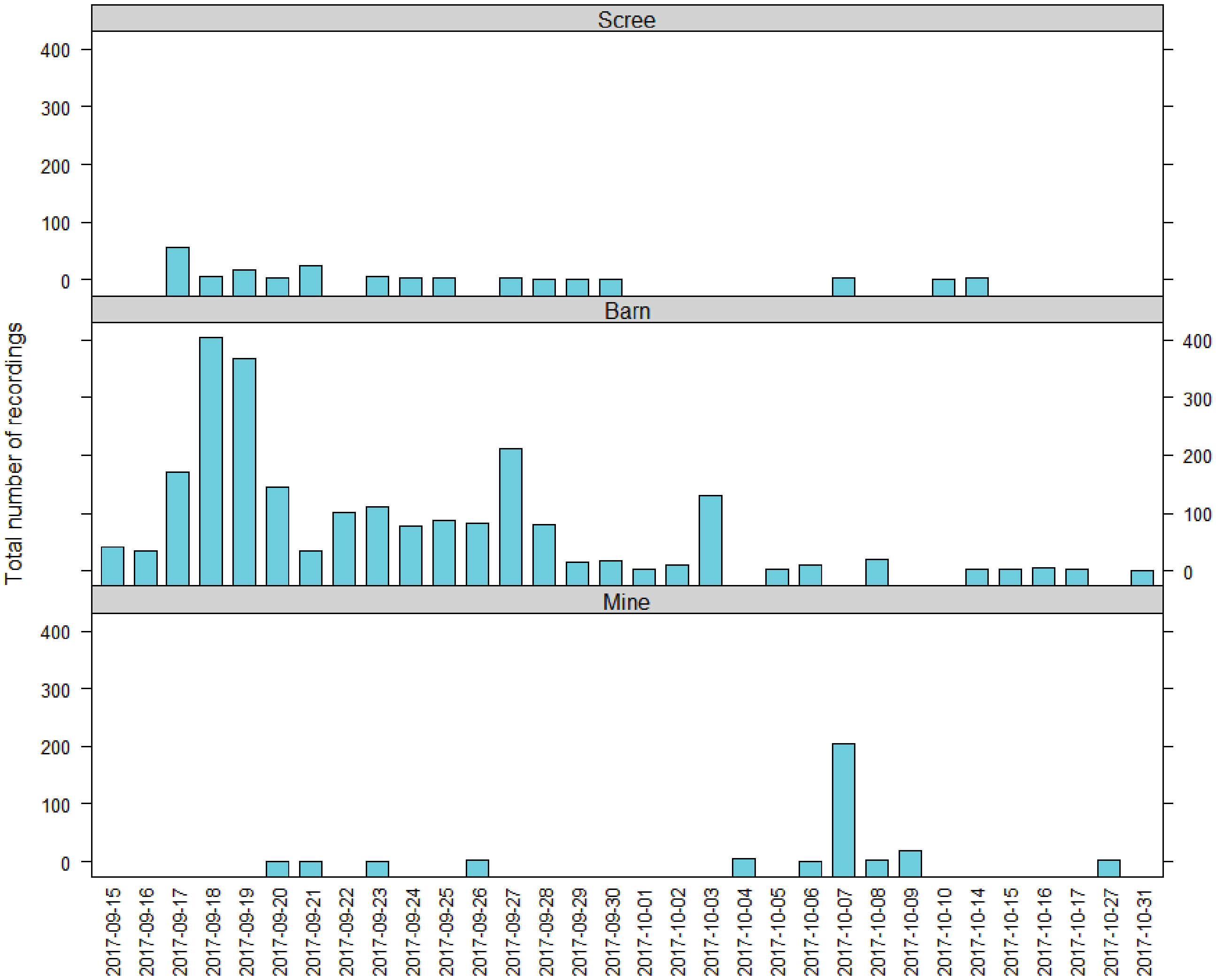

Figure 21. Total number of bat echolocation call recordings per night at the three sites; the mine, the barn and the scree over the deployment period. Note that not all days with zero recordings are included in the plot.

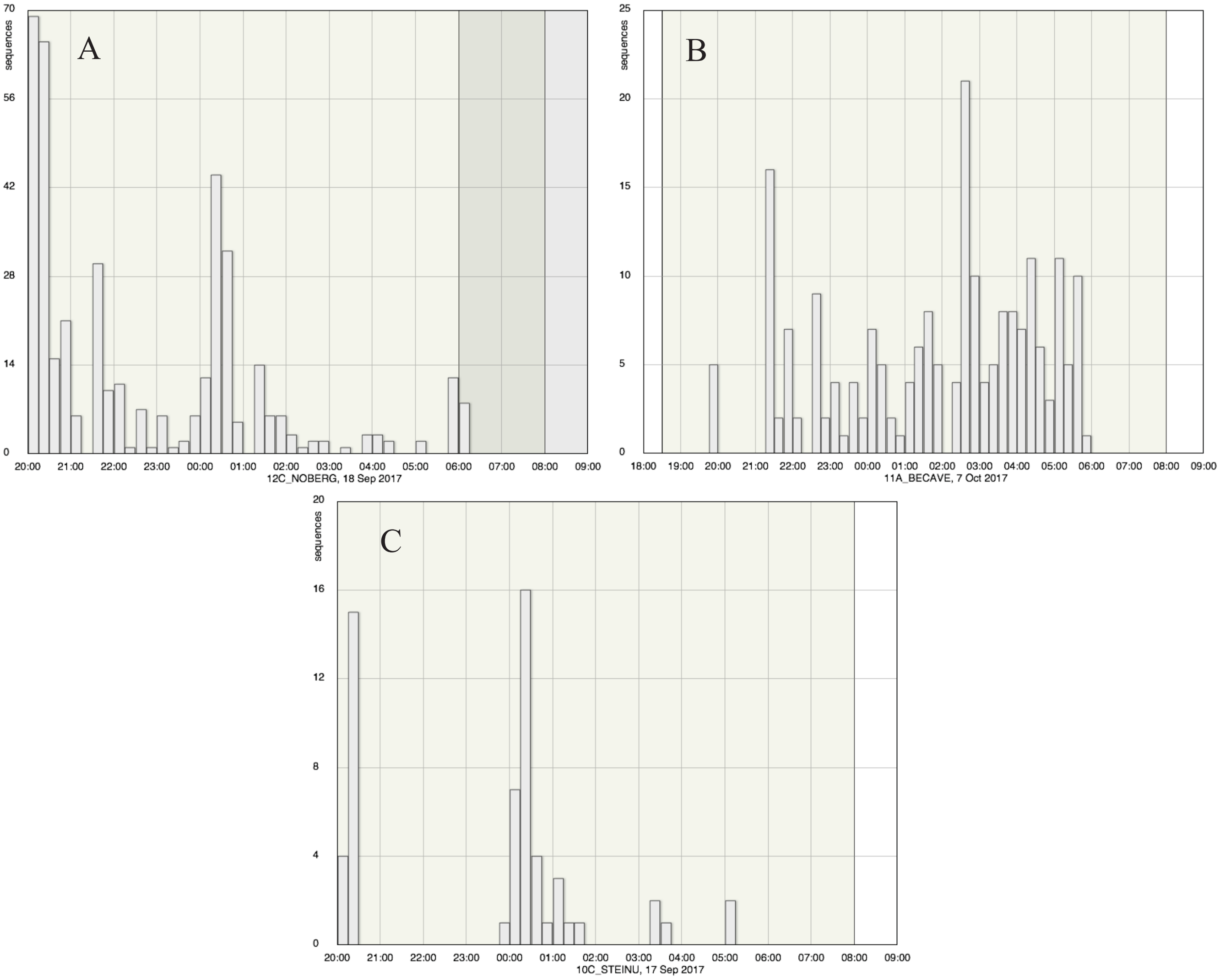

Figure 22. Activity bar charts from the highest activity nights at A) the barn, B) the mine and C) the scree. The figures show number of echolocation sequences recorded over time. Note that the recordings start at different times, and that the y axes have different lengths.

There was a lot more activity at the barn than at the other two batlogger deployment locations. During the night with the most activity (18.09.17), there were two main peaks of activity at this site; around 20:00 and 01:30 (Fig. 23, A). During the night with the most activity at the scree (07.10.17), the recordings were more spread out, but there were also two peaks; around 21:30 and 03:00 (Fig. 23, B). There was generally less activity at the scree, but during the night with the most activity (17.09.17), there were two peaks; around 20:00 and 00:30 (Fig. 23, C).

Discussion

Hibernacula in abandoned human-made mines

During the period of the fortnightly registrations in the mine at Sognsvann (2000-2010 and 2018), the bats generally arrived late October / early November, and left the mine late March / early April. Bats increase the frequency and duration of their torpor bouts later in the autumn, depending on the ambient temperature, food access etc. (Altringham, 1996). Late-born juveniles might need to hunt for a prolonged period to be able to acquire enough energy for the winter ahead (Frafjord, 2007). The mine was at its coldest temperature in the middle of winter (January - February), and this coincided with when the total number of bats was at its highest. Cold ambient temperatures make torpor bouts deeper and longer, and works as an energy saving strategy for bats hibernating in mines (Wermundsen et al., 2010).

Many European bat populations have experienced declining populations, particularly during the second half of the 20th century (Jones, 2009; Mickleburgh et al., 2002). However, in a report from the EEA (European Environmental Agency), where they use a prototype biodiversity indicator to study the population trends of 16 out of 45 bat species found at hibernation sites across the continent, they found that most bat species included seem to be increasing or stable in population numbers (1993 – 2011) (European Environmental Agency, 2013). Similar results were found in The National Bat Monitoring Programme in Great Britain, where they revealed a generally favorable picture for bats over the monitoring period (1997 – 2012); all the 10 species monitored showed a stable or increasing trend from at least one survey type (Barlow et al., 2015). This coincides with the results from the mines surveyed in this study; a significant increase in total number of bats since 1990 (Sognsvann, Djupdal, Røysåsen and Engelstadtjern), and stable numbers of bats in the remaining mines (Spenningsby, Alnsjø and Engelstadvang). It should be noted that neither the study from EEA (2013) nor the study from Barlow et al. (2015) included hibernacula data from mines in Norway. It should also be mentioned that there is an uncertainty connected to the mine counts, due to unexperienced observers and low numbers of observers during the early surveys of the mines included in this study, which may have caused an underestimation of bat numbers in these early years. The increases observed in total number of individuals hibernating in a mine over time, when the mine is only surveyed once a year, could also be explained by early or late registrations. If the mine is surveyed only in e.g. November or March, the number of bats will most likely be lower than the maximum number of hibernating bats there actually was in the mine that winter. If the mine surveys are done on a yearly basis, they should be carried out in the middle of winter, when the temperature is at its coldest to make sure that the maximum number of bats are registered. The installation of a gate in 2002, to keep people out of the mine at Sognsvann during winter, might also have had a positive effect on the number of bats opting to hibernate in this mine.

There are several physical factors that determine the selection of hibernacula, and the distribution and movement of bats inside a hibernaculum. The most important factors are temperature, humidity, air circulation, impact of the external climatic conditions, darkness and water flow (Klys et al., 2010). A complex mine with multiple tunnels, rooms, crevices, drilling holes etc., can provide a range of thermal habitats that benefit hibernating bats, and the ideal hibernacula offer a range of microhabitats (Perry, 2013). The six temperature loggers (10-60 meters) deployed inside the mine at Sognsvann during the winter of 2017-2018 showed a range of mean temperatures from 1.97 to 3.48 ºC. The logger that also registered humidity levels (10 meters) showed a mean humidity of 84.6 %. These observations fit well with the optimal temperature (2-10 ºC) and humidity (75-95 %) requirements for hibernating bats (Klys & Woloszyn, 2010; Meyer et al., 2016). Bats are susceptible to dehydration because of their relatively large, naked wing membranes and large lungs. Thus, bats tend to select hibernacula with high humidity and/or cluster together to reduce exposure of their skin to the ambient air (Perry, 2013).

There used to be a horizontal opening in what is now the end of the mine at Sognsvann. This opening was closed off and filled with rocks during a controlled blast in 1967, to avoid accidents where people could fall into the mine. However, this did not completely close the entrance, and there is still an airflow going through the mine. This is evident when looking at the temperature data from the logger deployed furthest into the mine (60 meters). Here, the range of temperatures are larger (less stable) and the mean temperature is lower than the logger at 40 meters, which shows that the external climatic conditions outside of the old horizontal opening still affect the inside of the mine. We also observe that there was a large drop in ambient temperature outside of the mine in late February, and that it negatively affected the temperature at all loggers inside of the mine.

The bats in the Sognsvann mine was found between 7.5 and 62 meters. This means that the bats can be found almost anywhere inside this hibernaculum, as the total length of the mine is 62 meters. However, most of the individuals were registered between 20 and 40 meters (mean distance to entrance for all registrations: 27.44 meters), which means that this stretch probably offers the most favorable climate in the mine. One possible explanation for why some bats were observed so close to the entrance is that later in the hibernation season, they have small energy reserves and are forced to minimize energy expenditure by moving to colder locations in the hibernaculum (Wermundsen & Siivonen, 2010). In this mine there has only been observed northern bats and Daubenton’s bats, but mainly the former. The northern bats were found throughout most of the mine, whilst the Daubenton’s bats (N=10) were found between 31 and 43.9 meters from the entrance. It is possible that bats are able to crawl through the rocks at the end of the mine, and hibernate in what used to be the rest of the mine. The number of bats hibernating in this mine could thus be larger than what has been observed.

Most of the registered bats in all the other mines were found less than 200 meters from the nearest entrance. The mean distance to the nearest entrance ranged from 35.9 to 165 meters. The mean number of individuals observed were lower in smaller mines, and larger in larger mines. This coincide with the findings of Smirnov et al. (2008), stating that the smaller the cave, the lower the total abundance of bats hibernating therein. The mines at Engelstadtjern and Engelstadvang both have total lengths of above 800 meters, but that includes all tunnels and branches. Due to their several entrances (Engelstadvang = 3, Engelstadtjern = 5), the furthest away from the entrance a bat can possibly get (max depth) is respectively 232 and 258.5 meters. The mine at Engelstadvang has a horizontal tunnel and two horizontal entrances approximately 15-20 meters above this tunnel (Fig. A11). This structure could generate a chimney effect, where air warmed by the cave exits top openings draws in cold air at the lower entrance (Perry, 2013), generally cooling down the inside of the mine. There could also be formed an equilibrium at some point between the upper and lower openings (Perry, 2013), and this could force bats to hibernate in these central parts of the mine. The remaining mines only have one entrance, and differ in max depth (53 – 663 meters). In all the mines, bats have been observed very close to the nearest entrance, with the smallest distance ranging between one and six meters away from the entrance. One possible explanation for this pattern is that these mines have only been surveyed one time during the winter, and if the survey was done during early or late winter, it might have been a bit warmer in the mines. This could mean that the more suitable temperatures were closer to the entrances.

In all the mines, the hibernating bats have exploited between 75 and 100 % of the max depth of the mines. The relatively small size of most of the mines included in this study could explain why the bats were found throughout most of the mines, as the differences in temperature might not be as big in small mines as in larger mines. Daan & Wichers (1967) found that in the deeper parts of the mine complex "Geulhemergroeve" in the Netherlands, the temperatures were above 10 ºC, which over time will not be suitable for a hibernating bat (Daan et al., 1967). Perry (2013) also found that the temperatures deeper in the "Great Scott Cave" in Missouri, USA were close to 12 ºC during most of the winter. In the Alnsjøen mine however, bats have been observed throughout 98% of the total length of the mine, even though the mine is 663 meters deep. There is a continuous stream of water running through this mine, and it could affect the climatic conditions. Water flow from the outside of a mine complex may increase or decrease the temperatures compared to the temperature outside of the mine (Perry, 2013). Cold water entering mines may lower the temperature, and thus equalize and stabilize the temperature gradient inside the mine. This can make the entire length of the mine suitable for hibernation, and it could explain why bats have been observed hibernating throughout the entire mine at Alnsjøen. The water that is entering in the far end of the mine is coming from the lowest point of the lake above. During winter, the highest density water of the lake will sink to the bottom and stay at 4 ºC. This will have a cooling effect on the deeper parts of the mine, and possibly a warming effect on the outermost part of the mine (Jeroen van der Kooij, pers. com.).

The general pattern of differences in species distribution in all mines included in this study was that whiskered/Brandt's bats and Daubenton's bats hibernated significantly further away from the entrances than northern bats and brown long eared bats. This coincides with the findings of Smirnov et al. (2008); in all artificial caves, the bat species found closest to the entrances were brown long eared bats and northern bats. It also coincides with findings from a study in Finland and Estonia, where northern bats and brown long eared bats hibernated in colder and drier locations, whereas whiskered/Brandt's bats and Daubenton's bats hibernated in warmer and more humid locations (Wermundsen, 2011). There were no significant differences in species distribution in the mines at Engelstadtjern and Røysåsen.

There was a significant negative relationship between number of individuals and temperature in the mine at Sognsvann when the snow cover was shallow (<30 cm). The snow cover is usually thinner during autumn and spring than during winter, and the temperature is at its coldest in the middle of winter. Seeing as the mine at Sognsvann used to have a horizontal opening that still affects the inside climate of the mine (airflow going through), a deep snow cover could have a negative impact on the airflow, whereas a shallow snow cover could let the air continue to flow through. The results show that there are less bats in the mine during higher temperatures, which makes sense as it is warmer during autumn and spring than during winter (when the number of hibernating bats is at its highest). They also show that a shallow snow cover enhances this negative relationship, and could be due to the fact that the hibernating bats are more exposed to the outside climatic conditions in the spring, working as a signal for the bats that the time has come to leave the hibernacula for the winter. The mine at Djupdalen, which also has a horizontal opening that has been filled by rocks, shows the same results as the mine at Sognsvann, and could be explained by the same theory. However, there are no significant relationships here. Generally, the relationship between temperature and snow cover at the remaining mines were varying or not significant. To my knowledge, there has been no previous studies on how snow cover affects bats before and during hibernation, and thus it is recommended for further research.

Roosts and activity in the autumn season

The 15 radio-tagged individuals of the autumn of 2017 led us to find 11 different roosting sites. Out of these 15 bats, 12 were brown long eared bats, two were Daubenton's bats, and one was a northern bat. We also captured one whiskered bat, but this individual was too small to carry a radio transmitter. The tagged bats used three different buildings (two houses, one cabin annex), two barns, three trees (all of them birch trees, one of which was deceased), two rock face crevices, and one abandoned mine (Spenningsby mine) as roosting sites during the autumn period. The first individual that was captured was a male brown long eared bat (#395), and this bat led us to find the barn at Nordre Berg, which turned out to be an important site for further capture of bats throughout the rest of the field period. Seven radio tagged brown long eared bats and one northern bat were found to use this barn as a roosting site throughout the autumn. On several occasions brown long eared bats were observed flying both on the inside of the barn cellar and the main room of the barn, and also crawling on the roof beams of the main room. Due to the fact that most of the tagged individuals in this study were brown long eared bats, the results are biased towards this species.

Bat species can be divided into four main forager groups: open-space aerial foragers, edge-space aerial/trawling foragers, narrow-space gleaning foragers, and narrow-space flutter-detecting foragers. The northern bat is an edge-space aerial forager, the Daubenton's bat is an edge-space trawling forager, and the brown long eared bat is a narrow-space gleaning forager (able to take prey from leaves of trees, bushes and directly from the ground) (Schnitzler et al., 2003;

Wermundsen et al., 2008). The bats' foraging strategies will determine which habitats they hunt in. Northern bats can be observed using a wide range of habitats as hunting grounds, suggesting that this species is a generalist with an opportunistic foraging behavior (Wermundsen & Siivonen, 2008). The only northern bat we captured (#285, male) was observed roosting in the barn where it was captured, and in a small annex building next to the barn. It was observed hunting around and above the barn, normally just after it had emerged from the roost at dusk. This individual was observed flying and hunting in a wide range of habitats; above fields, coniferous and mixed forests, close to and above a lake, above the main river going through Nittedal (Nitelva), and above the main road (Riksvei 4), which fits well with the edge-space aerial generalist forager description.

The 12 brown long eared bats that were captured and tagged used differing numbers of roost sites. Some of the individuals stayed in the same roost for a longer period, whereas others changed roosts every day. The first tagged brown long eared bat (#395) roosted in six different sites, ranging from buildings to rock face crevices. Another male (#106) switched between two roosting sites (attic of a wooden house and a birch tree), whereas most of the brown long eared bats roosted for a longer period in the barn where most of them were captured and tagged. Brown long eared bats have been recorded in a variety of wooded habitats, including orchards, parkland and conifer plantations, but there is evidence that broadleaved woodlands are preferred (Murphy et al., 2012). In Norway however, the majority of the forests are coniferous or mixed, which may force this species to hunt here. They tend to follow tree lines, hedges, overgrown banks and other lines of cover between the roost and the hunting grounds, and these routes can involve travelling distances greater than the most direct/shortest route would have done (Murphy et al., 2012). However, three brown long eared bats were observed crossing the main road in Nittedal (Riksvei 4) at 0.5 meters height (Rune Sørås, personal communication). If this is a reoccurring problem, it should be discussed whether installing green bridges or underpasses is needed to mitigate road mortalities. Such structures have the potential to allow bats to cross roads safely if they are built on already known commuting routes (Berthinussen et al., 2012). Brown long eared bats are food generalists, and have been found to utilize heterogenous foraging habitats. They seem to find a wide range of potential foraging sites in the vicinity of their roosts, and thus are not forced to move longer distances to find suitable foraging habitats (Ashrafi et al., 2013). We observed that this species foraged mostly in coniferous and mixed forests, but also around a lake (Bergstjern) and a clear cut, and around urban areas and fields.

It has been found that brown long eared bats have a restricted foraging range (<1 km from the roost), attributed to its slow flight as a consequence of the wing shape and wing loading of species adapted to a gleaning foraging strategy (Entwistle et al., 2000). In a study by Ashrafi et al. (2013), the maximum distance they observed this species away from the roost was 2.3 km, and thus we might expect brown long eared bats to travel shorter distances to swarming sites. However, brown long eared bats have been observed swarming 31 (Furmankiewicz & Altringham, 2006), 66 (Masing, 1989) and 88 (Gaisler et al., 2003) kilometers from the roost during autumn. We did not observe any bats travelling that far, but two male bats (#071 and #257) that were captured the same night at the scree (Holterkollen), were relocated respectively 6.2 km and 20 km east of the capture site. This confirms that brown long eared bats are able to travel longer distances, despite their slow flight. #071 was located several days after capture, during a car search, roosting in a horse barn in Gjerdrum municipality. The radio transmitter of #257 was relocated in Sørum municipality during an airplane radio tracking, 11 days after the capture, where it was lost in a mixed forest. It is possible that the observation of these individuals at the scree was part of some sort of swarming behavior, where they examined the scree as a potential overwintering site or were looking for potential mates from a different colony than their own, which could promote gene flow between bat colonies and increase the genetic diversity (Veith et al., 2004).

The female Daubenton’s bat #317 was captured underneath a bridge, and was observed hunting above the river surface north and south of the capture bridge. We have reason to believe that this individual roosted in at least three different roosts, seeing as this individual was observed coming from the south of the only located roost site (dead birch tree 15 meters from the river bank, approximately 1 km north of the capture site) − whilst an observer was standing there at one occasion − and from the north on another occasion. Day roost switching in Daubenton’s bats has been found earlier (Parsons et al., 2003), but here they found that no bats used more than two different roosts during their observations. Our observations suggest that #317 had more than two day roosts, but it could be due to the bat moving outside of the reach of the receiver, and thus appearing to be emerging from more than two roosts. It has been found that Daubenton’s bats use cavities that are humid. Natural cavities arise in humid conditions which allow the wood to rot. Daubenton’s bats might favor natural cavities for this reason (Boonman, 2000). This description fits well to the deceased birch tree, which we observed #317 to use as roost site.

Michaelsen et al. (2013) found that both northern bats and whiskered bats used rock scree as roosts after their hunting activity ended in late autumn, and that a northern bat with fitted with a transmitter with a long-lasting battery lifetime was recorded in a rock scree until early January. This study suggests that bats roosting in screes at high altitudes are likely to be snowed in as early as October. The snow cover can have an insulating effect on bats hibernating here (Michaelsen et al., 2013). Frafjord (2007) found that northern bats used rock face crevices and rock screes as roosting sites during autumn in Troms county. They hypothesized that bats are most likely spread out in various underground sites during the hibernation period. Several studies from North America have found evidence of bats roosting in ground-level rock crevices, rock fields along mountain slopes (talus slopes) and at the base of canyon walls during spring – autumn (Johnson et al., 2016; Moosman et al., 2015). Moosman et al. (2015) found that bats exhibited a hibernation-like pattern of torpor in the middle of March on talus slopes (scree) in Virginia, and thus suggest that these bats may also overwinter in this habitat. There has also been documented calls of bats in December (early hibernation period) near rock outcrops (exposed rock faces) in Nebraska, which suggests that they were hibernating here (Lemen et al., 2016). One of the tagged brown long eared bats (#395, male) in this study, roosted in two different rock face crevices, but did not stay in the respective roosts for more than one day each. We did not observe any bats roosting in rock screes or crevices for prolonged periods during the autumn.

Radio telemetry worked well for locating autumn roost sites: based on radio-tagging and tracking of 15 radio-tagged bats, we identified 11 different roost sites. However, the approach proved very challenging for finding hibernacula sites, and despite considerable efforts and resources, it yielded little empirical data. There are no GPS transmitters small enough to be used on the species of bats that we tracked during the study period. Traditional VHF transmitters have rather limited detection ranges, and this makes locating and tracking bats more challenging, especially when the bats move quickly from one area to another. The study area was quite challenging to move around in, due to dense forests, bogs, challenging topography and sometimes low accessibility by vehicle. Our triangulation efforts could have been better with a more precise and coordinated effort, like they did in Bontadina et al. (2002), where two field workers coordinated their simultaneous bearings using trigger signals from watches and remained in contact using hand-held FM-radios (Bontadina et al., 2002). Our rock scree transmitter test showed that the reach of the signal from our radio transmitters was very short. The signal was easily attenuated/blocked when the transmitter was hidden behind rocks in the scree, and did not reach further than 15-30 meters. This shows that if any bats roosted in rock screes, it would have been extremely difficult to locate them, without tracking the bats to the location. We also had issues with transmitters falling off the tagged individuals. Four of the 15 radio transmitters were relocated, and two transmitters were found, but their exact position was not determined. All the relocated transmitters had been fitted to brown long eared bats. On four occasions, the radio transmitters were found in/beneath coniferous trees. One of the relocated transmitters had been torn off the individual, as the battery pack on the inside of the transmitter was visible. Brown long eared has relatively long fur compared to other Norwegian species (Jeroen van der Kooij, pers. com.), and this difference may potentially cause transmitters fitted to this species to be more easily torn off the bat inside of colonies and roosts. Later in the season, the bats appeared more stationary and stayed in the roost rather than emerge to forage. Several of the bats that were captured at the barn late in autumn, were not observed hunting at all, and suddenly disappeared after a number of days roosting in the barn. It is likely that these bats stayed in the barn due to low temperatures, and that they were waiting for a short-term rise in temperature to build up their fat storage before travelling to the hibernacula.

The three automatic echolocation recorders that we deployed yielded different results with respect to total bat activity. There was a significant decrease in total number of bat recordings at the barn and at the scree over the deployment period, as you would expect later in the autumn, due to lower temperatures and lower abundance of insects (Czenze et al., 2017). There was a lot more activity at the barn than at the two other sites, probably because this site was used for roosting throughout the autumn. The batlogger deployed at the mine (Spenningsby) was unfavorably placed (behind some trees, not expedient for the purpose) from the day of deployment (29.09.17) until 04.10.17, and this might have negatively influenced its ability to record echolocation calls of bats flying in front of the mine. Three days after it was moved away from the trees and closer to the mine entrance, there was a large peak in activity at this site (07.10.17). This peak in activity, that lasted from 20:00 to 06:00, might have been caused by a swarming event, where bats gather to mate and to pass on information about suitable hibernacula to their young (Furmankiewicz & Altringham, 2006; Piksa, 2008; van Schaik et al., 2015; Veith et al., 2004). There was apparently generally little activity at the scree. One possible explanation for this is that the batlogger was facing in the wrong direction. The batlogger was facing west, away from the rocks. This could have negatively affected the number of recordings. However, this batlogger recorded its maximum number of bat recordings (57) on the first night of deployment (17.09.17), and we observed quite a lot of activity at the scree at that time (using bat detectors). Seeing as this was the same night as we captured and tagged the two brown long eared bats (#071 and #257) that travelled far away from the scree, it strengthens the theory of this activity being a swarming event.

Conclusion and conservation implications

Underground sites such as caves and mines are crucial to the survival of many bat species worldwide, and may be threatened by resumption of activities such as open cast mining, sealing of abandoned mines, and poorly managed tourism developments (e.g. “Blaafarveverket” mine complex) (Mickleburgh et al., 2002). The mine hibernacula located in Norway are relatively small, and consequently the number of bats per hibernaculum is low. Therefore hibernation sites used by even a small number of bats are important, and should be taken into account in land use planning (Wermundsen, 2011). Swarming sites are also of importance, as they can serve as mating sites and information centers (Lemen et al., 2016; Michaelsen et al., 2013; Veith et al., 2004).

The main objective of this study was to identify roost sites, roost site characteristics and hibernacula during autumn. I wanted to find out whether radio telemetry is a good method for finding roost sites and hibernacula during autumn in Norway. I also wanted to find out if automatic logging of echolocalization calls can give additional information about bat activity and swarming behaviour. Radio telemetry worked well for locating autumn roost sites, but proved challenging for finding hibernacula during autumn; despite considerable efforts and resources, this approach yielded little empirical data on hibernacula. Automatic bat echolocation logging worked well for recording general bat activity, and it also recorded events that could be evidence of swarming behavior in front of a mine and a scree.

Currently, we are still lacking important knowledge needed for making good management decisions and to implement effective conservation measures for bats in Norway. It is of critical importance to identify habitats used for maternity colonies, hibernation, hunting, and for movement between these areas, and we need to focus research on these topics to ensure evidence-based management and conservation of bats.

References

Altringham, J. D. (1996). *Bats: Biology and Behaviour*: Oxford University Press.

Ashrafi, S., Rutishauser, M., Ecker, K., Obrist, M. K., Arlettaz, R., & Bontadina, F. (2013). Habitat selection of three cryptic Plecotus bat species in the European Alps reveals contrasting implications for conservation. *Biodiversity Conservation*. doi:10.1007/s10531-013-0551-z

Barlow, K. E., Briggs, P. A., Haysom, K. A., Hutson, A. M., Lechiara, N. L., Racey, P. A., . . . Langton, S. D. (2015). Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation, 182*, 14-26. doi:10.1016/j.biocon.2014.11.022

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1-48. doi:10.18637/jss.v067.i01

Berthinussen, A., & Altringham, J. (2012). Do bat gantries and underpasses help bats cross roads safely? *PLoS One, 7*(6). doi:10.1371/journal.pone.0038775

Bivand, R. S., Keitt, T., & Rowlingson, B. (2017). rgdal: Bindings for the 'Geospatial' Data Abstraction Library.

Bontadina, F., Schofield, H., & Naef-Daenzer, B. (2002). Radio-tracking reveals that lesser horseshoe bats forage in woodland. *Journal of Zoology, 258*, 281-290. doi:10.1017/S0952836902001401

Boonman, M. (2000). Roost selection by noctules and daubentons bats. *Journal of Zoology, 251*, 385-389.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling, 197*, 516-519.

Crawley, M. J. (2013). *The R book (2nd ed.)*. Chichester, West Sussex, United Kingdom: Wiley.

Czenze, Z. J., Brigham, R. M., Hickey, A. J., & Parsons, S. (2017). Cold and alone? Roost choice and season affect torpor patterns in lesser short-tailed bats. *Oecologia, 183*(1), 1-8. doi:10.1007/s00442-016-3707-1

Daan, S., & Wichers, H. J. (1967). Habitat selection of bats hibernating in a limestone cave. *Biodiversity heritage library*, 1-26.

European Environmental Agency. (2013). *European bat population trends: A prototype biodiversity indicator*. Retrieved from EEA Technical report, https://www.eea.europa.eu/:

Frafjord, K. (2007). Possible hibernation sites of the Northern bat Eptesicus nilssonii at its northern range limit in Norway. *Fauna, 60*(3-4), 246-254.

Frafjord, K. (2013). Influence of night length on home range size in the northern bat Eptesicus nilssonii. *Mammalian Biology - Zeitschrift für Säugetierkunde, 78*(3), 205-211. doi:10.1016/j.mambio.2012.06.005

Furmankiewicz, J., & Altringham, J. (2006). Genetic structure in a swarming brown long-eared bat (Plecotus auritus) population: evidence for mating at swarming sites. *Conservation Genetics, 8*(4), 913-923. doi:10.1007/s10592-006-9246-2

Gaisler, J., Hanák, V., Hanzal, V., & Jarský, V. (2003). Výsledky kroužkování netopýrů v České republice a na Slovensku. *Vespertilio, 7*, 3-61.

Haarsma, A.-J. (2008). *Manual for assessment of reproductive status, age and health in European Vespertilionid bats*.

Henriksen, S., & Hilmo, O. (2015). *Norsk rødliste for arter 2015*. Retrieved from

Hijmans, R. J. (2017). raster: Geographic Data Analysis and Modeling.

Isaksen, K., Klann, M., van der Kooij, J., Michaelsen, T. C., Olsen, K. M., Starholm, T., Sunding, C. F., Sunding, M. F. og Syvertsen, P. O. (2009). Flaggermus i Norge. Kunnskaps-status og forslag til nasjonal handlingsplan. *Norsk Zoologisk Forening. Rapport 13.*, 124.

Johnson, J. S., Treanor, J. J., Lacki, M. J., Baker, M. D., Falxa, G. A., Dodd, L. E., . . . Lee, E. H. (2016). Migratory and winter activity of bats in Yellowstone National Park. *Journal of Mammalogy*, gyw175. doi:10.1093/jmammal/gyw175

Jones, G., Jacobs, D. S., Kunz, T. H., Willig, M. R., Racey, P. A. (2009). Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research, 8*, 93-115. doi:10.3354/esr00182

Klys, G., & Woloszyn, B. W. (2010). Ecological aspects of bat hibernacula. *Travaux du Muséum National d'Histoire Naturelle, 53*, 489–497. doi:10.2478/v10191-010-0034-3

Lemen, C. A., Freeman, P. W., & White, J. A. (2016). Acoustic evidence of bats using rock crevices in winter: A call for more research on winter roosts in North America. *Transactions of the Nebraska Academy of Sciences, 36*, 9-13. doi:10.13014/K2SF2T3Q

Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. *R News, 2*(3), 18-22.

Masing, M. (1989). Bat research and bat protection in Estonia. *European bat research 1987: Fourth European Bat Research Symposium, Praha 1987*, 343−347.

Meyer, G. A., Senulis, J. A., & Reinartz, J. A. (2016). Effects of temperature and availability of insect prey on bat emergence from hibernation in spring. *Journal of Mammalogy, 97*(6), 1623-1633. doi:10.1093/jmammal/gyw126

Michaelsen, T. C. (2016). Summer temperature and precipitation govern bat diversity at northern latitudes in Norway. *Mammalia, 80*(1), 1-9. doi:10.1515/mammalia-2014-0077

Michaelsen, T. C., Jensen, K. H., & Högstedt, G. (2011). Topography is a limiting distributional factor in the soprano pipistrelle at its latitudinal extreme. *Mammalian Biology - Zeitschrift für Säugetierkunde, 76*(3), 295-301. doi:10.1016/j.mambio.2010.12.004

Michaelsen, T. C., Olsen, O., & Grimstad, K. J. (2013). Roosts used by bats in late autumn and winter at northern latitudes in norway. *Folia Zoologica*, 297-303.

Mickleburgh, S. P., Hutson, A. M., & Racey, P. A. (2002). A review of the global conservation status of bats. *Oryx, 36*(01). doi:10.1017/s0030605302000054

Moldal, T., Vikoren, T., Cliquet, F., Marston, D. A., van der Kooij, J., Madslien, K., & Orpetveit, I. (2017). First detection of European bat lyssavirus type 2 (EBLV-2) in Norway. *BMC Vet Res, 13*(1), 216. doi:10.1186/s12917-017-1135-z

Moosman, P. R., Warner, D. P., Hendren, R. H., & Hosler, M. J. (2015). Potential for Monitoring Eastern Small-footed Bats on Talus Slopes. *Northeastern Naturalist, 22*(1), NENHC-1-NENHC-13. doi:10.1656/045.022.0102

Murphy, S. E., Greenaway, F., Hill, D. A., & Bennett, N. (2012). Patterns of habitat use by female brown long-eared bats presage negative impacts of woodland conservation management. *Journal of Zoology, 288*(3), 177-183. doi:10.1111/j.1469-7998.2012.00936.x

Ngamprasertwong, T., Piertney, S. B., Mackie, I., & Racey, P. A. (2014). Roosting Habits of Daubenton's Bat (Myotis daubentonii) during Reproduction Differs between Adjacent River Valleys. *Acta Chiropterologica, 16*(2), 337-347. doi:10.3161/150811014x687297

Parsons, K. N., & Jones, G. (2003). Dispersion and habitat use by Myotis daubentonii and Myotis nattereri during the swarming season: implications for conservation. *Animal Conservation, 6*(4), 283-290. doi:10.1017/s1367943003003342

Pebesma, E. J., & Bivand, R. S. (2005). Classes and methods for spatial data in R. *R News, 5*(2).

Perry, R. W. (2013). A review of factors affecting cave climates for hibernating bats in temperate North America. *Environmental Reviews, 21*(1), 28-39. doi:10.1139/er-2012-0042

Piksa, K. (2008). Swarming of Myotis mystacinus and other bat species at high elevation in the Tatra Mountains, southern Poland. *Acta Chiropterologica, 10*(1), 69-79. doi:10.3161/150811008x331108

R Core Team. (2017). R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing, Vienna, Austria*.

Rydell, J., Nyman, S., Eklöf, J., Jones, G., & Russo, D. (2017). Testing the performances of automated identification of bat echolocation calls: A request for prudence. *Ecological Indicators, 78*, 416-420. doi:10.1016/j.ecolind.2017.03.023

Rydell, J., Strann, K. B., & Speakman, J. R. (1994). First record of breeding bats above the Arctic Circle: northern bats at 68-70°N in Norway. *Journal of Zoology, 233*(2), 335-339. doi:10.1111/j.1469-7998.1994.tb08597.x

Schnitzler, H.-U., Moss, C. F., & Denzinger, A. (2003). From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology & Evolution, 18*(8), 386-394. doi:10.1016/s0169-5347(03)00185-x

Smirnov, D. G., Vekhnik, V. P., Kurmaeva, N. M., Shepelev, A. A., & Il'in, V. Y. (2008). Spatial Structure of the community of bats (Chiroptera: Vespertilionidae) hibernating in artificial caves of Samarskaya Luka. *Biology Bulletin, 35*(2), 211-218. doi:10.1134/s1062359008020167

Stone, E. L., Jones, G., & Harris, S. (2013). Mitigating the effect of development on bats in England with derogation licensing. *Conserv Biol, 27*(6), 1324-1334. doi:10.1111/cobi.12154

van der Kooij, J., & Olsen, K. M. (2012). Kartlegging og overvåkning av flaggermus i Norge - Forpliktelser, metodikk og historikk. *Norsk Zoologisk Forening, 15*, 1-85.

van Schaik, J., Janssen, R., Bosch, T., Haarsma, A. J., Dekker, J. J., & Kranstauber, B. (2015). Bats Swarm Where They Hibernate: Compositional Similarity between Autumn

Swarming and Winter Hibernation Assemblages at Five Underground Sites. *PLoS One, 10*(7), e0130850. doi:10.1371/journal.pone.0130850

Veith, M., Beer, N., Kiefer, A., Johannesen, J., & Seitz, A. (2004). The role of swarming sites for maintaining gene flow in the brown long-eared bat (Plecotus auritus). *Heredity (Edinb), 93*(4), 342-349. doi:10.1038/sj.hdy.6800509

Wermundsen, T. (2011). Bat habitat requirements – implications for land use planning. *Dissertationes Forestales, 111*, 1-49.

Wermundsen, T., & Siivonen, Y. (2008). Foraging habitats of bats in southern Finland. *Acta Theriologica, 53*(3), 229–240.

Wermundsen, T., & Siivonen, Y. (2010). Seasonal variation in use of winter roosts by five bat species in south-east Finland. *Open Life Sciences, 5*(2). doi:10.2478/s11535-009-0063-8

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution, 1*(1), 3-14. doi:10.1111/j.2041-210X.2009.00001.x

Appendix

Table A1. *Myotis*, *Plecotus* and *Eptesicus* bats captured during the field period, N = number of bats captured of each species at each date and location. If more than one individual was captured, body mass and forearm length are reported as range (minimum - maximum). Note that only a subset of these captured and measured bats were radio-tagged (see Table 3).

Date	Location	UTM32V_E	UTM32V_N	Species	N	Mass (g)	Forearm length (mm)
23.08.2017	Spenningsby mine	606555	6662598	*P. auritus*	2	7.3 – 7.8	38.5 – 40.4
				M. daubentonii	1	11.0	39.3
28.08.2017	Nordre Berg barn	605094	6662048	*E. nilsonii*	1	9.0	37.4
				P. auritus	2	7.3 – 9.1	37.4 – 39.8
12.09.2017	Nordre Berg barn			*P. auritus*	5	5.7 – 9.5	37.0 – 39.8
				M. mystacinus	1	4.9	34.2
17.09.2017	Holterkollen scree	607084	6657549	*P. auritus*	3	7.5 – 7.9	37.4 – 39.4
24.09.2017	Li bridge	607782	6654168	*M. daubentonii*	1	8.8	37.2
26.09.2017	Nordre Berg barn	605114	6662057	*P. auritus*	2	6.9 – 7.4	37.6 – 39.2
15.10.2017	Nordre Berg barn			*P. auritus*	1	7.6	39.1
16.10.2017	Nordre Berg & Spenningsby mine			*P. auritus*	2	8.3 – 9.8	38.6 – 39.6
Autumn				*M. daubentonii*	2	8.8 – 11.0	37.2 – 39.3
				E. nilsonii	1	9.0	37.4
				M. mystacinus	1	4.9	34.2
				P. auritus	17	5.7 – 9.8	37.0 – 40.4
Total					21		

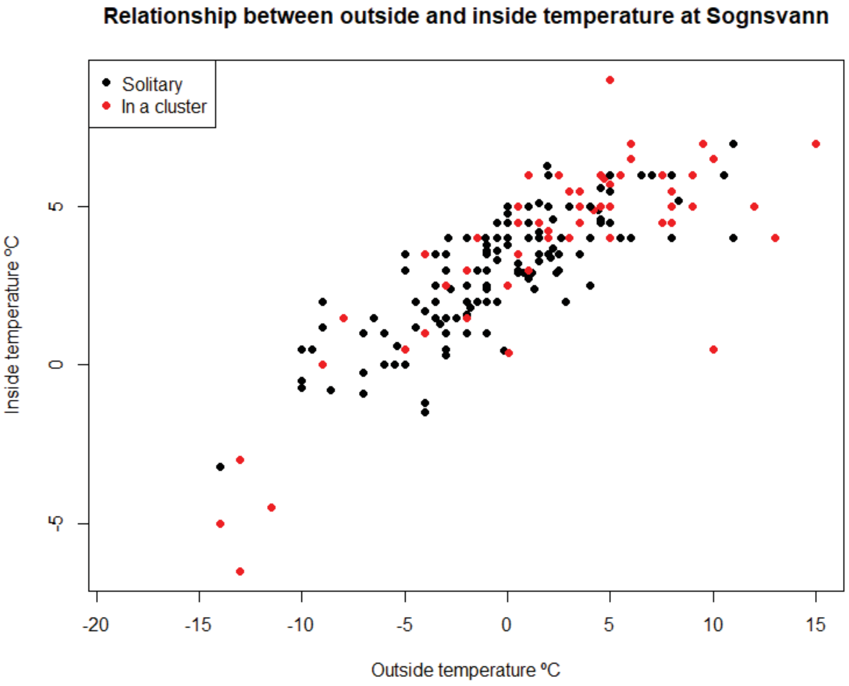

Figure A1. The relationship between temperature measured inside and outside the mine at Sognsvann. Red dots denote clusters of bats with two or more individuals, and black dots denote solitary bats.

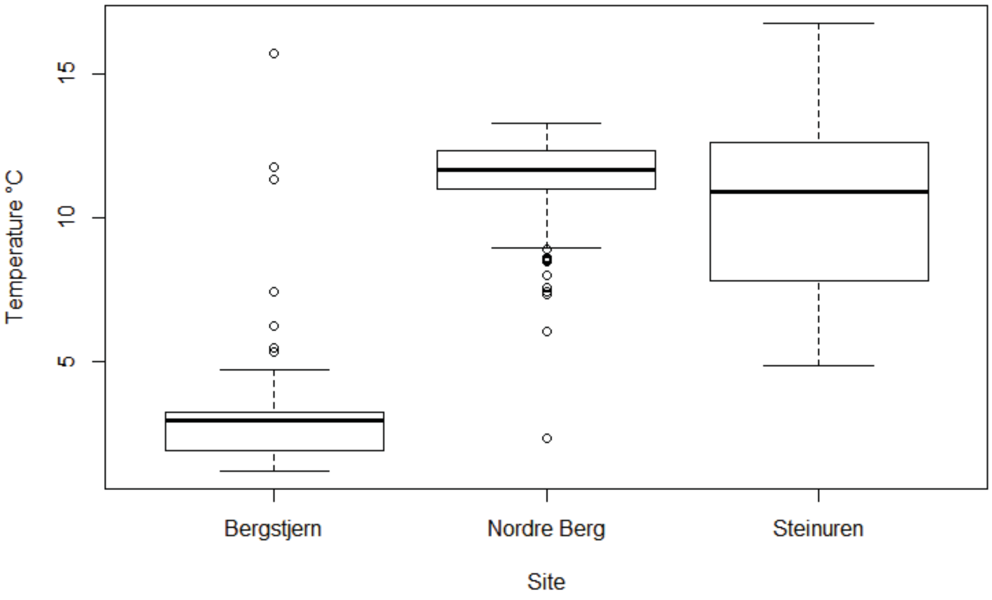

Figure A2. Temperature (ºC) measurements at the three batlogger sites (September – November).

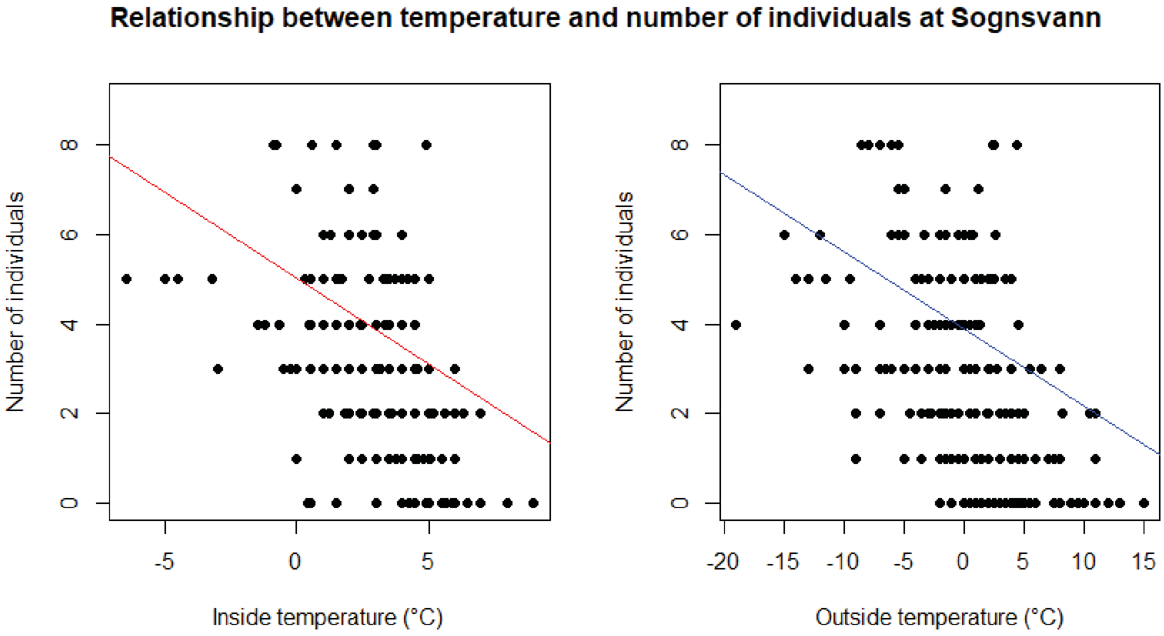

Figure A3. Relationship between the number of bat individuals observed inside the Sognsvann mine and temperature inside (left panel) and outside (right panel) the mine. Red and blue lines = lines of best fit.

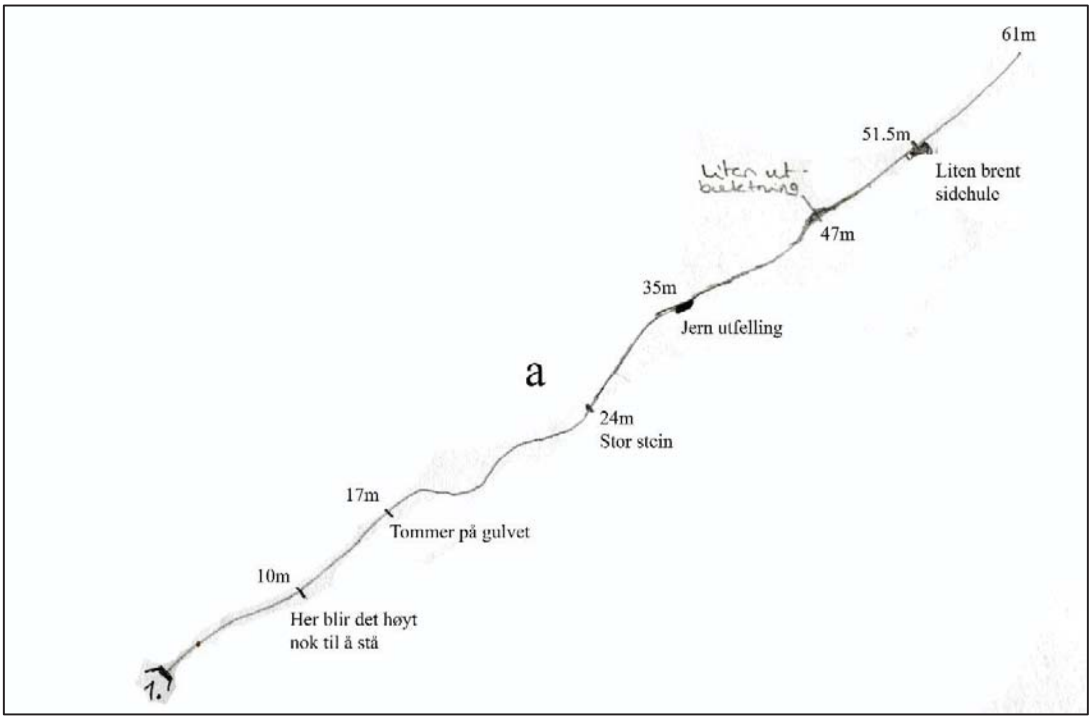

Figure A4. Sketch of the mine at Sognsvann.

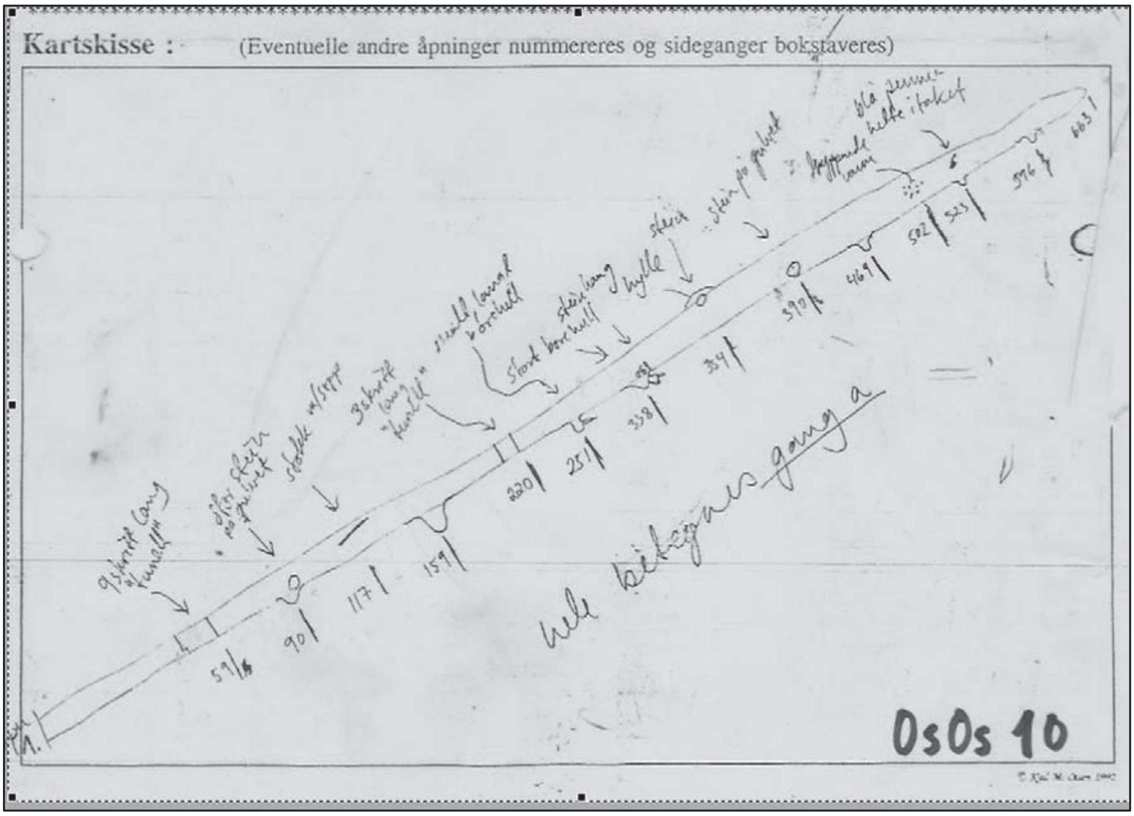

Figure A5. Sketch of the mine at Alnsjøen.

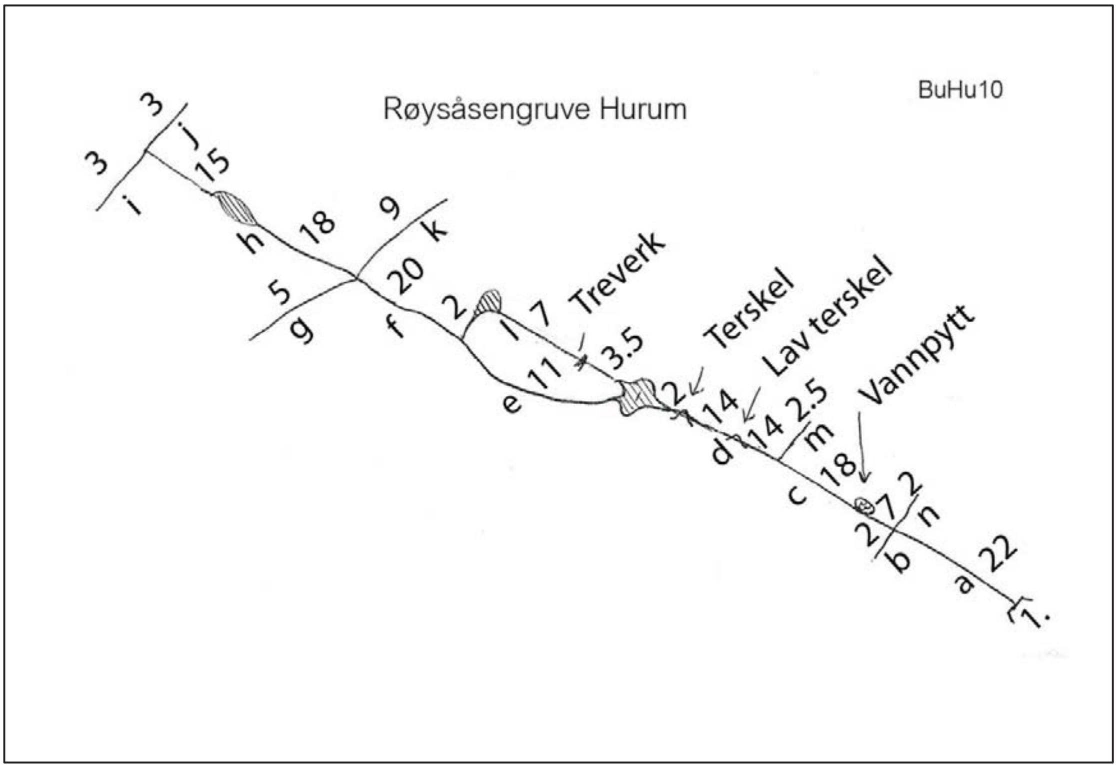

Figure A6. Sketch of the mine at Røysåsen.

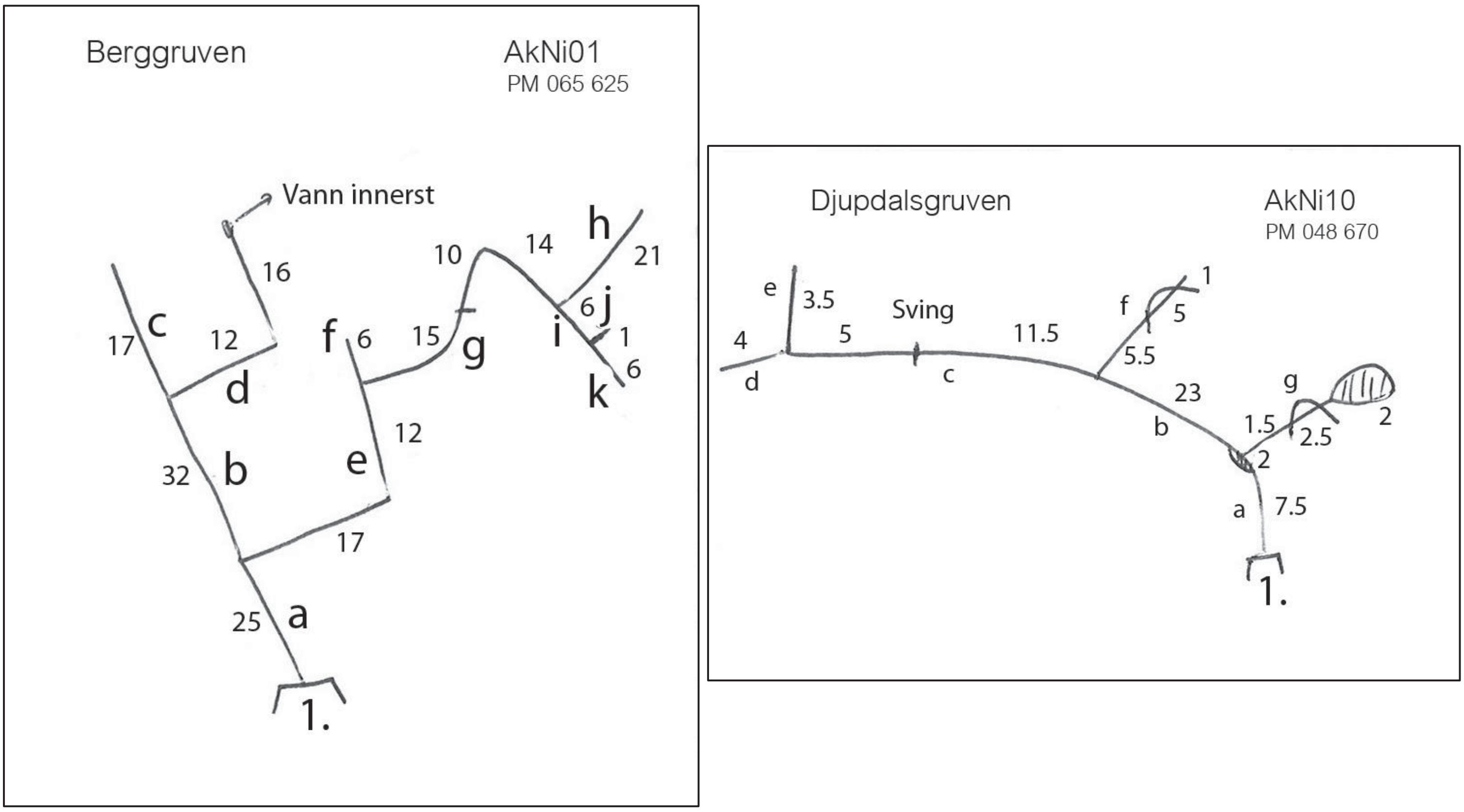

Figure A7 & A8. Sketches of the mines at Spenningsby (left) and Djupdal (right).

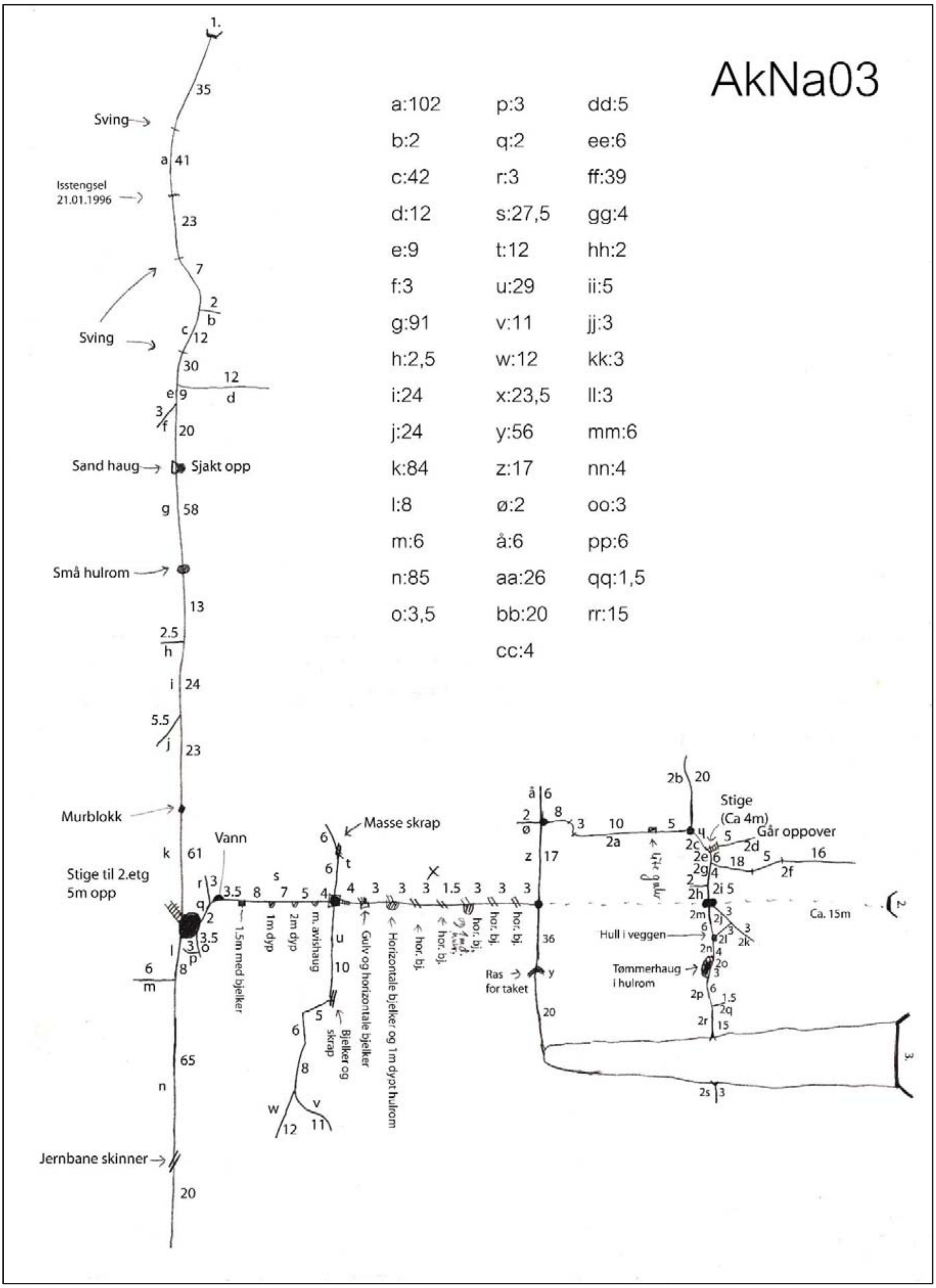

Figure A9. Sketch of the mine at Engelstadvang. Letter and number (a-rr) represent the length of each branch/tunnel.

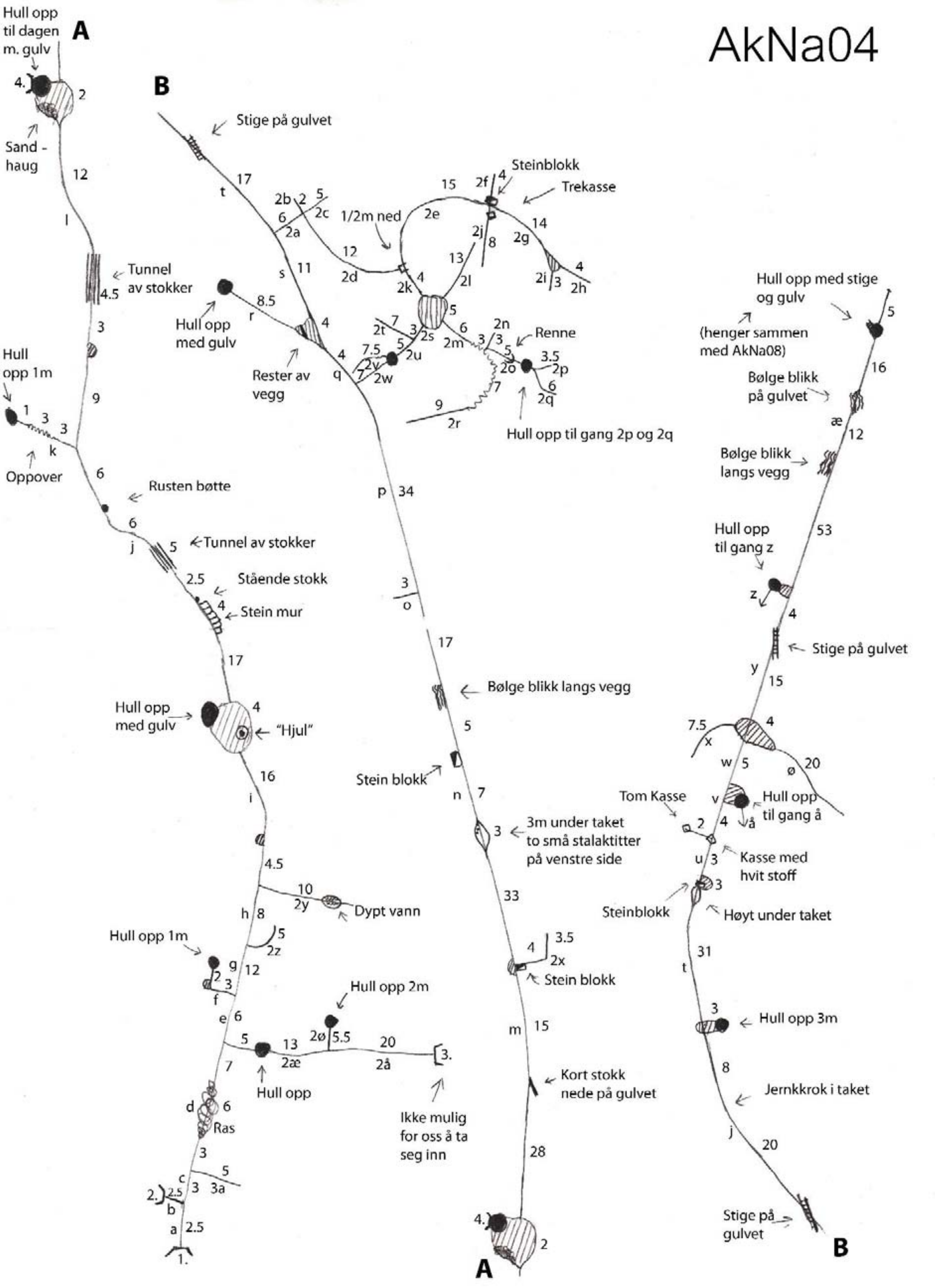

Figure A10. Sketch of the mine at Engelstadtjern.

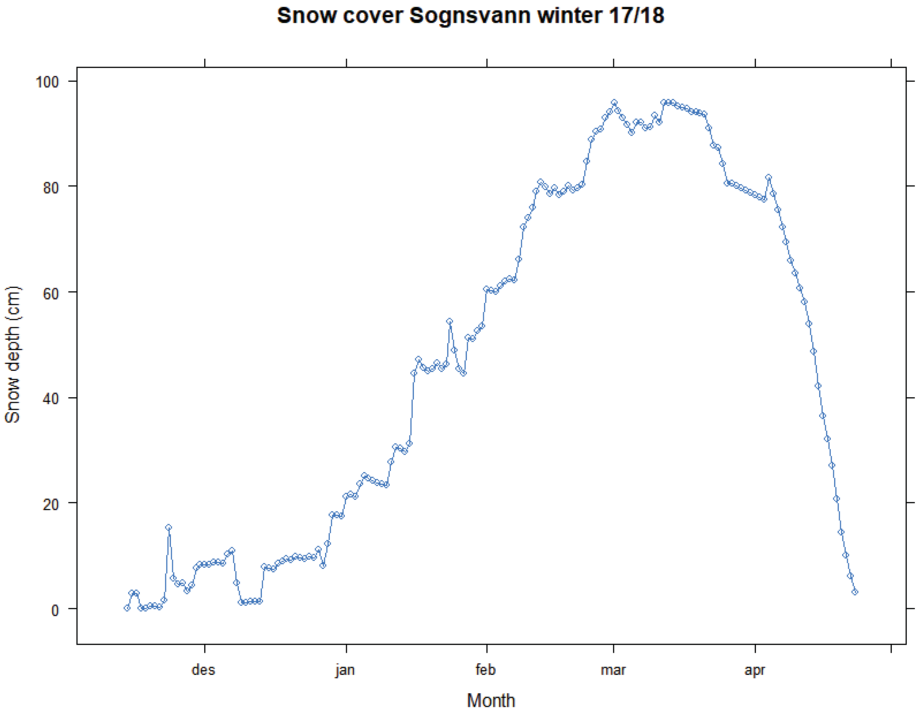

Figure A11. Snow depth (cm) at the Sognsvann mine during the winter of 2017-18.

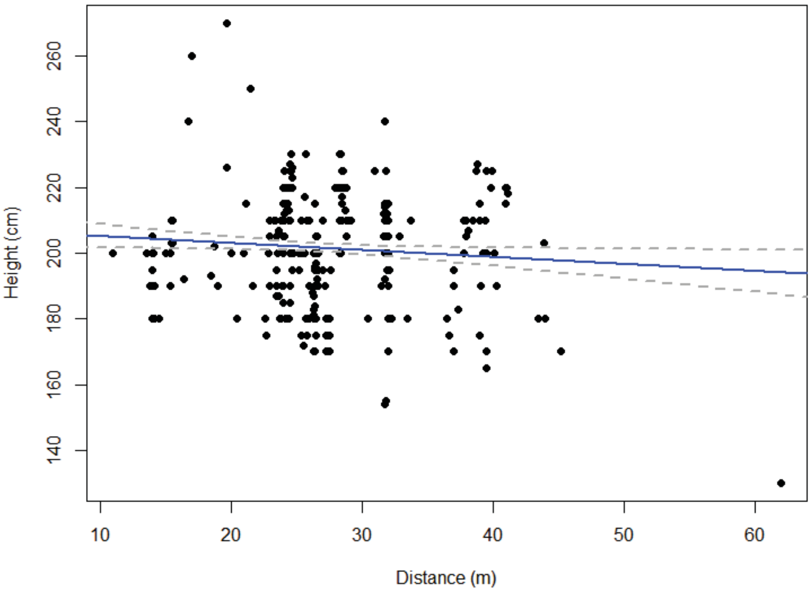

Figure A12. The relationship between the height (cm) at which the bats were observed (on the wall of the mine) and the distance (m) to the mine entrance at Sognsvann. Blue line = Estimated relationship. Grey stapled lines = 95 % confidence intervals.

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