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Bat habitat requirements – implications for land use planning

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Academic dissertation

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ABSTRACT

Knowledge of the habitat requirements of bat species is needed in decision making in land use planning. Bats' hibernation requirements were studied both in Estonia and in southern Finland. In both countries, the northern bat and the brown long-eared bat hibernated in colder and drier locations, whereas Daubenton's bat and Brandt's/whiskered bats hibernated in warmer and more humid locations. In Estonia, the pond bat hibernated in the warmest and most humid conditions, whereas Natterer's bat hibernated in the coldest and driest conditions.

Hibernacula were at their coldest in mid-season and became warmer towards the end of the season. The results suggest that bats made an active choice of colder hibernation temperatures at the seasons end. They minimised the negative effects of hibernation early in the hibernation season by hibernating in warmer locations and energy expenditure late in the hibernation season by hibernating in colder locations.

The use of foraging habitats was studied in northern and southern Finland. The northern bat used foraging sites opportunistically. Daubenton's bat foraged mainly in water habitats, whereas Brandt's/whiskered bats and the brown long-eared bat foraged mainly in forest habitats. In northern Finland, Daubenton's bats foraged almost exclusively on rivers and typically together with the northern bat. Daubenton's bats and Brandt's/whiskered bats were found only where there were lower ambient light levels. One of the most important things in the management of foraging areas for them is to keep them shady.

Hibernacula in Finland typically housed few bats, suggesting that hibernation sites used by even a small number of bats are important. Bats typically used natural stone for hibernation suggesting that natural underground sites in rocks or cliffs or man-made underground sites built using natural stone are important for them. The results suggest that appropriate timing of surveys may vary according to the species and latitude.

Keywords: *Eptesicus*, *Myotis*, *Plecotus,* foraging habitats, winter roots, hibernation, seasonal variation

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Espoo, October 2010

Terhi Wermundsen

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by seven research articles. These papers are reproduced with the permission of the journals in question and are referred to in the text by their Roman numerals.

I Siivonen, Y. and Wermundsen, T. 2003. First records of *Myotis dasycneme* and *Pipistrellus pipistrellus* in Finland. Vespertilio 7: 177–179.
http://www.ceson.org/publikace.php

II Wermundsen T. and Siivonen Y. 2008. Foraging habitats of bats in southern Finland. Acta Theriologica 53: 229–240.
http://acta.zbs.bialowieza.pl

III Siivonen Y. and Wermundsen T. 2008. Characteristics of winter roosts of bat species in southern Finland. Mammalia 72: 50–56.
DOI: 10.1515/MAMM.2008.003

IV Siivonen Y. and Wermundsen T. 2008. Distribution of Natterer's bat (*Myotis nattereri*) in Finland. Nyctalus 13: 42–47.
http://nyctalus.com

V Siivonen Y. and Wermundsen T. 2008. Distribution and foraging habitats of bats in northern Finland: *Myotis daubentonii* occurs above the Arctic Circle. Vespertilio 12: 41–48.
http://www.ceson.org/publikace.php

VI Wermundsen T. and Siivonen Y. 2009. Seasonal variation in use of winter roosts by five bat species in south-east Finland. Central European Journal of Biology 5: 262–273.
DOI: 10.2478/s11535-009-0063-8

VII Wermundsen T. and Siivonen Y. A comparison of the hibernation patterns of seven bat species in Estonia. Lutra. In press.
http://www.zoogdiervereniging.nl/node/42

AUTHOR'S CONTRIBUTION

Paper I: The author carried out the observations and wrote the paper together with the co-author.

Papers II, VI, and VII: The author planned the measurements and carried out them in the field together with the co-author. The author was responsible for the statistical analysis and for writing the manuscript and acted as corresponding author.

Paper III: The author planned the measurements and carried them out in the field together with the co-author. The author was responsible for the statistical analysis and for writing the manuscript.

Paper IV: The author planned the measurements, carried out them in the field, and analysed them together with the co-author. The author was responsible for writing the manuscript.

Paper V: The author planned the measurements with the co-author and participated in the data collection. The author was responsible for writing the manuscript.

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1 INTRODUCTION

1.1 Bats in international environmental law

Finland is a signatory to the Bern Convention on the Conservation of European Wildlife and Natural Habitats 1979 (SopS 29/1986) and the Agreement on the Conservation of Populations of European Bats (EUROBATS) 1991 (SopS 104/1999). The Bern Convention requires strict protection measures for species listed in Appendix II. This appendix includes all bat species except the common pipistrelle (*Pipistrellus pipistrellus* Schreber, 1774*)*, which is listed in Appendix III. The Agreement on the Conservation of Populations of European Bats was set up under the auspices of the Convention on the Conservation of Migratory Species of Wild Animals 1986 (Sops 62/1988). This convention lists all bat species in Appendix II, indicating that they are migratory species which may be subject to Agreements. The fundamental obligations of EUROBATS are listed below.

1. Each Party shall prohibit the deliberate capture, keeping, or killing of bats except under permit from its competent authority.

2. Each Party shall identify those sites within its own area of jurisdiction which are important for the conservation status, including the shelter and protection, of bats. It shall, taking into account as necessary economic and social considerations, protect such sites from damage or disturbance. In addition, each Party shall endeavour to identify and protect important feeding areas for bats from damage or disturbance.

3. When deciding which habitats to protect for general conservation purposes, each Party shall give due weight to habitats that are important for bats.

4. Each Party shall take appropriate measures to promote the conservation of bats and shall promote public awareness of the importance of bat conservation.

5. Each Party shall assign to an appropriate body responsibilities for the provision of advice on bat conservation and management within its territory, particularly with regard to bats in buildings. Parties shall exchange information on their experiences in this matter.

6. Each Party shall take such additional action as it considers necessary to safeguard populations of bats which it identifies as being subject to threat and shall report under Article VI on the action taken.

7. Each Party shall, as appropriate, promote research programmes relating to the conservation and management of bats. Parties shall consult each other on such research programmes, and shall endeavour to co-ordinate such research and conservation programmes.

8. Each Party shall, wherever appropriate, consider the potential effects of pesticides on bats, when assessing pesticides for use, and shall endeavour to replace timber treatment chemicals which are highly toxic to bats with safer alternatives.

The IUCN Red List of Threatened Species provides taxonomic, conservation status, and distribution information on plants and animals that have been globally evaluated using the IUCN Red List Categories and Criteria. This system is designed to determine the relative risk of extinction, and the main purpose of the IUCN Red List is to catalogue and highlight those plants and animals that are facing a higher risk of global extinction (i.e. those listed as Critically Endangered, Endangered, and Vulnerable). The global conservation status of all European bat species has been evaluated by IUCN (IUCN 2010).

1.2 Bats in EU environmental law

The aim of Council Directive 92/43/EEC of 21 May on the conservation of natural habitats and of wild fauna (Habitats Directive) is to "maintain or restore, at favourable conservation status, natural habitats and species of wild fauna and flora of Community interest". According to Article 12, it is prohibited to disturb these species in Annex IV (a) particularly during the period of breeding, rearing, hibernation, and migration. Furthermore, causing the deterioration or destruction of breeding sites or resting places of Annex IV (a) species is prohibited. All insectivorous bats in Europe are listed in Annex IV (a) of the Habitats Directive, which means that all Finnish bat species are "species of Community interest in need of strict protection". The pond bat (*Myotis dasycneme* Boie, 1825) is also listed in Annex II as a species of "Community interest whose conservation requires the designation of special areas of conservation (SACs)". These areas belong to a network of protected sites across the European Union called Natura 2000.

1.3 Bats in national environmental law

1.3.1 Nature Conservation Act

Bats are protected by the Finnish Nature Conservation Act (1096/1996). According to Section 39 (Protection Provisions), the following prohibitions apply to all specimens belonging to a protected species:

1) deliberate killing and capture;
2) appropriation, removal, or deliberate destruction of eggs and other developmental stages in their life cycles;
3) deliberate disturbance of animals, particularly during breeding, in important resting places during migration, or any other sites of significance to their life cycles.

According to Section 49, "the destruction and deterioration of breeding sites and resting places used by specimens of animal species referred to in Annex IV (a) of the Habitats Directive is prohibited". In special cases the local authority (Centres for Economic Development, Transport, and the Environment) is authorised to grant derogations from the prohibition.

According to Section 46 (Threatened Species), "any naturally occurring species whose survival in the wild is at risk in Finland can be declared a threatened species by decree". According to Section 47 (Species Under Strict Protection), "any species at imminent risk of extinction can be placed under a strict protection order by a decree. The Finnish Ministry of Environment shall, as necessary, prepare a programme for reviving the populations of such species. The causing of deterioration and destruction of a habitat important for the survival of a species under strict protection is prohibited. Natterer's bat (*Myotis nattereri* Kuhl, 1818) is the only bat species in Finland that has been declared a threatened species, whose survival in the wild is at risk and which has been placed under strict protection by a decree at the national level (Rassi et al. 2001).

The breeding and resting places of bats include maternity colonies, as well as summer and winter roosts. In summer, females aggregate in maternity colonies, where babies are born. Typical maternity colonies and summer roosts are in buildings, hollow trees, bird- and bat-boxes, and under bridges (e.g. Mitchell-Jones et al. 1999). Typical winter roosts are underground sites such as military installations and fortifications, cellars, ice-houses, storage facilities, abandoned mines, tunnels, and natural caves (Mitchell-Jones et al. 2007). The breeding and resting places may be threatened when old trees are cut down, old houses are demolished, or underground sites destroyed.

Foraging areas and commuting routes are significant sites for bats and especially the EUROBATS Agreement underlines that important feeding areas should be identified and protected for bats from damage or disturbance. All European bats feed primarily on insects, but the insect species eaten, hunting territories, and hunting strategies vary from species to species (Mitchell-Jones et al. 1999). Bats use landmarks such as tree lines, hedgerows, overgrown banks, forest edges, and water edges to commute from one place to another. These areas are typically rich in insects and bats use them as foraging areas as well (Limpens et al. 1991).

1.4 Biodiversity impact assessments

1.4.1 Land Use and Building Act

The objective of the Finnish Land Use and Building Act (1999/132) is to ensure that the use of land and water areas and building activities promote ecologically sustainable development. According to Section 5 (Objectives in land use planning), "the objective in land use planning is to promote, through adequate assessment of impact, biological diversity and other natural values, as well as environmental protection". According to Section 9 (Impact assessment in connection with planning), plans must be based on adequate studies and reports. When a plan is drawn up, the environmental impact of implementing the plan must be assessed to the necessary extent. Such an assessment must cover the entire area where the plan may be expected to have a material impact.

1.4.2 Act on Environmental Impact Assessment Procedure

According to the Act on Environmental Impact Assessment Procedure (468/1994), the environmental impacts of all projects that may be expected to have considerable negative environmental impacts must be assessed.

1.4.3 Act on the Assessment of the Effects of Certain Plans and Programmes on the Environment

According to the Act on the Assessment of the Effects of Certain Plans and Programmes on the Environment (200/2005), the environmental impacts of plans and programmes must be assessed if these may have significant environmental impacts.

1.4.5 Nature Conservation Act

According to Section 65 (Assessment of Projects and Plans), "If a project or plan, either individually or in combination with other projects and plans, is likely to have a significant adverse effect on the ecological value of a site included in, or proposed by the Council of State for inclusion in, the Natura 2000 network, and the site has been included in, or is intended for inclusion in, the Natura 2000 network for the purpose of protecting this ecological value, the project's planner or implementer is required to conduct an appropriate assessment of its impact. The same shall correspondingly apply to any project or plan outside the site which is liable to have a significantly harmful impact on the site." The above assessment of impact can also be carried out as part of the assessment procedure referred to in Chapter 2 of the Act on Environmental Impact Assessment Procedure (468/1994).

1.4.6 Bat surveys for impact assessments

Impact assessments are based on ecological baseline studies. During the baseline studies existing data are collected and new data generated by biodiversity survey work. The data are analysed, interpreted, and reported (Söderman 2003). As bats are strictly protected in Finland, the impact of plans, projects, and programmes on them should be analysed beforehand. A survey for bats should be indicated when background information on distribution and occurrence suggests that they may be present. The first bat survey for land use planning in Finland was conducted in 2001 in the city of Järvenpää (Siivonen 2001). The present standard used to define the areas important to bats on the map, and to classify these areas into three categories to show the priority conservation areas, was established in 2005 by the city of Helsinki (Siivonen 2004). The areas categorised as important to bats in Finland include maternity colonies, summer and winter roosts, foraging areas, and commuting routes (Siivonen 2004). So far, the majority of bat surveys in Finland have been carried out in the summer. Thus knowledge on areas important to bats in wintertime is urgently needed. The bat species that exist in Finland and their conservation status are presented in Table 1.

1.5 Hibernation requirements

In autumn, insectivorous bats in temperate regions accumulate body fat (energy reserves), which they use while hibernating during winter, when food is scarce or unavailable. Bats hibernate to minimise energy expenditure during winter, but hibernation has ecological and physiological costs (Table 2).

Bats can minimise the costs by minimising the time spent in hibernation. The hibernation period is not continuous but is normally interrupted by brief periods of arousal (Lyman et al. 1982). Arousals represent 80–90% of the total cost of hibernation, because bats must raise their body temperature to euthermic levels (Thomas et al. 1990). Internal (physiological) and external (climatic) stimuli initiate arousals during the hibernal period (Dorgelo and Punt 1969). During arousals bats feed (e.g. Avery 1985), drink (Thomas and Geiser 1997), copulate, or change hibernation sites (Ransome 1968).

Table 1. Finnish bat species and their conservation status at the national and international levels (Rassi et al. 2001, EUROBATS 2009, Finnish Environmental Institute 2010, IUCN 2010). The IUCN categories to assess the conservation status of species can be different at the national and international levels.
The common pipistrelle, the parti-coloured bat, the pond bat, the pygmy bat, and the serotine are not classified in IUCN categories at the national level
(*LC= least concerned, DD=data deficient, EN=endangered, NT=near threatened, **only one observation in Finland).

		Conservation status							
		National level			European Union Habitats Directive		International level		
Latin name	English name	Protected by Conservation Act	Threatened species Strict protection by a decree	IUCN categories at national level*	Annex II	Annex IV	IUCN Red List of Threatened Species*	Bern Convention Appendices	Bonn Convention (EUROBATS)
Myotis brandtii (Eversmann, 1845)	Brandt's bat	x		DD		x	LC	II	x
Myotis dasycneme (Boie, 1825)	Pond bat	x		–	x	x	NT	II	x
Myotis daubentonii (Kuhl, 1817)	Daubenton's bat	x		LC		x	LC	II	x
Myotis mystacinus (Kuhl, 1817)	Whiskered bat	x		DD		x	LC	II	x
Myotis nattereri (Kuhl, 1817)	Natterer's bat	x	x	EN		x	LC	II	x
Pipstrellus nathusii (Keyserling & Blasius, 1839)	Nathusius' pipistrelle	x		DD		x	LC	II	x
Pipstrellus pipistrellus (Schreber, 1774)	Common pipistrelle	x		–		x	LC	III	x
Pistrellus pygmaeus (Leach, 1825)**	Pygmy pipistrelle	x		–		x	LC	II	x
Nyctalus noctula (Schreber, 1774)	Noctule	x		DD		x	LC	II	x
Eptesicus nilssonii (Keyserling & Blasius, 1839)	Northern bat	x		LC		x	LC	II	x
Eptesicus serotinus (Schreber, 1774)**	Serotine	x		–		x	LC	II	x
Plecotus auritus (Linnaeus, 1758)	Brown long-eared bat	x		LC		x	LC	II	x
Vespertilio murinus (Linnaeus, 1758)	Parti-coloured bat	x		–		x	LC	II	x

Table 2. Ecological and physiological costs of hibernation.

	Costs of hibernation	References
Ecological costs		
	Decreased detection of predators	Humpries et al. 2003
	Increased likelihood of freezing	Clawson et al. 1980
Physiological costs		
	Decreased immune response	Luis and Hudson 2006
	Reduced motor function	Choi et al. 1998
	Reduced protein synthesis	Frerichs et al. 1998
	Sleep deprivation	Daan et al. 1991

The body temperature of hibernating bats is near the ambient temperature. A shortened period of hibernation is made possible by hibernating in warmer ambient temperatures, which causes higher body temperatures during hibernation and therefore leads to shorter bouts of hibernation (Wojciechowski et al. 2007). Hibernating in warmer temperatures increases energy expenditure and this option is therefore restricted to individuals with large fat stores (Munro et al. 2005, Boyles et al. 2007). Bats with small fat stores must concentrate on saving energy, and consequently select colder temperatures for hibernation (Boyles et al. 2007). Colder bodies during hibernation lead to longer bouts of hibernation. Humidity is also an important microclimatological factor for hibernating bats. Bats have no special provision to reduce loss of water during hibernation. Therefore many species select sites with high humidity (Thomas and Cloutier 1992, Lausen and Barclay 2006).

Bats choose optimal temperatures for hibernation either by shifting their locations within hibernacula or by moving among hibernacula (Ransome 1968, Daan 1973, Bogdanowicz and Urbańczyk 1983, Masing 1984, Kokurewicz 2004), but the range of temperatures available within potential hibernacula limits this choice. Bats seem to prefer hibernacula with a variation in temperature (Mitchell-Jones et al. 2007, Boyles et al. 2007).

The temperatures at which bats hibernate are species-specific, although intra-species (Nagel and Nagel 1991, Webb et al. 1996) and seasonal variation (Hitchcock 1949, Twente 1955, Ransome 1968, Daan 1973, Webb et al. 1996, Kokurewicz 2004) exist as well. Some bat species use thermally stable sites, while others prefer more variable ones (Brack 2007). Hibernating in crevices reduces water loss and provides insulation from the external environment, especially from airflow (Hock 1951). Evaporation occurs more rapidly when the air is dry. When the air is saturated, no evaporation occurs. Airflow increases evaporation rates by transporting water vapour away from the evaporating surface. It also increases evaporation when transporting warmer or drier air from surrounding areas to displace the moist, cool air above an irrigated surface (Louw 1993).

Webb et al. (1996) reviewed the hibernal temperatures of 34 bat species, and found large inter- and intra-specific variation in the temperatures at which bats hibernated. Differences in body fat reserves may cause intra-species variation in hibernation temperatures (Boyles et al. 2007) and consequently in other hibernation requirements. As body fat reserves get lower and lower towards spring, bats may use different strategies (minimising the costs of hibernation vs. minimising energy expenditure) throughout the hibernation period. At the beginning of the hibernation season bats may tend to use warmer areas (large energy reserves) to minimise the costs of hibernation and at the end of the season they may use colder areas (smaller energy reserves) to minimise energy expenditure. Masing (1982) suggests that bat species hibernate in colder conditions in northern Europe than their conspecifics in Central Europe. The higher the latitude, the shorter the day, the colder the climate during winter, and the longer the winter. Therefore in the north bats may be forced to minimise energy expenditure, while in Central Europe they rather tend to minimise the costs of hibernation.

Webb et al. (1996) suggest that species with a more northerly distribution are able to hibernate in colder conditions than species with a more southerly distribution. This would mean that species with a more northerly distribution tend to save energy (spend more time in hibernation), while species with a more southerly distribution tend to minimise the costs of hibernation (spend less time in hibernation). Among the seven bat species studied in this thesis, the northern distribution border of the pond bat clearly runs further south than those of the other six species, while that of the northern bat clearly runs further north than those of the other six species. In Europe, the pond bat occurs north of 60° N (IUCN 2010). The northern bat frequently occurs above the Arctic Circle (Siivonen and Sulkava 1999, IUCN 2010). Daubenton’s bat is one of the most common bat species in Europe, with a range spanning from 63° N in Fennoscandia (Nyholm 1965, Ahlén and Gerell 1989). The distribution of the brown long-eared bat reaches to 63–64° N, and one individual has even been found in Hiipinä, Russia (67° N; Siivonen and Sulkava 1999). Brandt’s bat and the whiskered bat can be found up to 65° N (Siivonen and Sulkava 1999). Natterer’s bat occurs up to 63° N in Sweden, but there this species is rare and its occurrence very patchy (Ahlén 2004, IUCN 2010).

As the body temperature of hibernating bats is near the ambient temperature, the benefit of clustering (reduced heat loss) is highest during arousals (Clawson et al. 1980, Arnold 2007, Boyles et al. 2008). Bats that have shorter bouts of hibernation may concentrate on saving energy during arousals and subsequent periods of euthermy, i.e. they may have a tendency to cluster. Clustering behaviour is also species-specific (e.g. Twente 1955, McNab 1974, Clawson et al. 1980, Brack 2007).

1.6 Use of foraging habitats

Insectivorous bats use echolocation to search for food, to commute from one place to another, and to avoid obstacles (Griffin 1958). Bats emit calls out to the environment and listen to the echoes of those calls that return from various objects in the environment. Echolocation calls are adapted to the particular environment, hunting behaviour, and food source of the species. Bat species echolocate within frequency ranges that suit their foraging environment and prey types.

The echolocation pulses, foraging modes, preferred foraging habitats, and predominant prey types of Brandt’s bat, Daubenton’s bat, the whiskered bat, Natterer’s bat, the northern

Table 3. Echolocation signals, foraging modes, preferred foraging habitats, and predominant prey type of the six bat species (Swift and Racey 1983, Rydell 1986, 1989, Beck 1995, de Jong 1995, Anderson and Racey 1991, Shiel et al. 1991, Siemers and Schnitzler 2000, Siemers et al. 2001a, Swift and Racey 2002, IUCN 2010) studied in this thesis.

Species	Echolocation pulses in search flight	Foraging modes	Preferred foraging habitat	Predominant prey type
Brandt's bat	Steep FM	Aerial	Between trees	Moths (Lepidoptera), small flies (Diptera)
Daubenton's bat	Steep FM	Trawling, aerial	Over water surfaces (woodland: between trees)	Small flies (Diptera:Chironomidae)
Whiskered bat	Steep FM	Aerial, (gleaning)	Between trees	Small flies (Diptera), spiders (Arachnida), moths (Lepidoptera)
Natterer's bat	Steep FM	Aerial, gleaning	Close to vegetation	Larger flies (Diptera), spiders (Arachnida), moths (Lepidoptera)
Northern bat	Shallow FM	Aerial	Open and edge habitats	Small flies (Diptera), moths (Lepidoptera), beetles (Coleoptera)
Brown long-eared bat	Steep FM	Gleaning, aerial	Within vegetation	Moths (Lepidoptera), beetles (Coleoptera), caddies flies and long-horned flies (Trichoptera), spiders (Arachnida)

bat, and the brown long-eared bat are presented in Table 3. The echolocation calls of all six bat species are composed of frequency-modulated (FM) components. This type of call contains a downward sweep through a range of frequencies. FM pulses can be steep or shallow. A steep pulse is spread across many frequencies. Because the energy of the call is spread out among many frequencies, the distance at which a bat can detect targets is limited (Fenton 1995a). These pulses are shorter in duration and work best in close, cluttered environments (with large amounts of background noise) because they enable the bat to emit many calls extremely rapidly without overlap (confusing which echo corresponds to which call). Steep pulses permit the precise range discrimination, or localisation, of the target at shorter distances (Simmons & Stein 1980). Bats that search for prey among vegetation, e.g. the *Myotis* and *Plecotus* species, use only broadband FM signals both for ranging and detection. FM bats that forage in open areas or in edge habitats often add a narrowband component at the end of the call where the frequencies are lowest. A narrow sweep is spread across a few frequencies. Therefore energy is focused just on a few frequencies, which facilitates the detection of distant objects (Neuweiler 1989). These bats can adjust their echolocation behaviour according to the habitats in which they forage, which enables them to be flexible in their use of foraging habitats (Fenton 1990, Schnitzler and Kalko 1998, 2001).

Bats are able to see and may also use visual cues in addition to sonic cues when searching for food. Brown long-eared bats and northern bats have been found to use their vision in searching for food in Sweden (Eklöf et al. 2002, Eklöf & Jones 2002). Bats' vision typically works better at dusk and dawn than in bright daylight (Bradbury & Nottebohm 1969, Ellins & Masterson 1974).

Wing shape further determines the type of habitats in which a species can forage. Bats with long, narrow wings are fast fliers and typically hunt in open environments (Baagøe 1987). Bats with short, broad wings with a relatively large wing surface fly slowly. They are best suited for hunting in dense vegetation or in landscapes with numerous obstacles (Baagøe 1987).

Different bat species may forage in the same habitat (Rydell 1989, Barataud 1990, Fluckiger and Beck 1995, Gaisler et al. 1996, Haupt et al. 2006). In this case, the diet or the foraging techniques of these species usually differ to some extent, perhaps to avoid competition (Rydell 1986, Shiel et al. 1991, Beck 1995, Swift 1998, Haupt et al. 2006). Bats catch insects by gleaning, aerial hawking, or trawling (Schnitzler and Kalko 1998). Gleaning means that bats take their prey from a surface. When gleaning, bats usually do not use echolocation in searching for food, but they listen to prey-generated acoustic cues (Schnitzler and Kalko 2001). Trawling means that bats glean insects from the water surface by using their feet and/or their tail membrane. Aerial hawking means that bats pursue and catch their prey in flight. The majority of vespertilionid bats are flexible in their diets (e.g. Kunz 1974, Fenton 1995b, Swift 1998), so they usually eat what is available in the habitat where they forage (Swift 1998). The availability of prey in a habitat depends on the habitat, weather conditions, and air temperature, as well as the time of the year and time of the night (Jones and Rayner 1988, Swift 1998, Kalko and Schnitzler 1989, Rydell et al. 1999). The lightness of summer nights may further restrict the possibility of hunting in a habitat because the risk of predation is higher at higher light levels (Nyholm 1965, Rydell et al. 1996).

Bats tend to use linear landscape elements as landmarks when commuting from one place to another (Limpens & al. 1991). Linear landscape elements are features that form a long line or are narrow in shape, such as lanes, hedges, hedgerows, tree lines, forest edges, rivers, canals, and streams. Species with steep FM pulses, such as Daubenton's bats, closely follow linear landscape elements in their flight path. The insect density of linear landscape elements, especially vegetation borders, is usually high and therefore bats also forage in linear habitats (Limpens et al. 1991).

1.7 Aims of the study

The aim of this thesis is to improve our knowledge of the habitat requirements of non-migratory bat species (i.e. species that hibernate in Finland) in order to make it easier to manage and conserve areas important for them. Land use planning seeks to order and regulate the use of land, ensuring that land is used efficiently for the benefit of the economy, population, and the environment. Land use planners should take areas used by bats into account in the preparation and adoption of plans, programmes, and projects. Studies I, III, IV, VI, and VII determine the hibernation requirements of bats in Finland and Estonia, whereas studies II, IV, and V describe the foraging habitats used by bats in Finland.

Knowledge of bat habitat requirements both in the summer and the winter is vital for bat management and conservation, because areas known to be of significance for bats can be excluded from development. No studies have been conducted on bat hibernation habitats in Finland. The only study on the summer foraging areas of Finnish bats was published in 1965 (Nyholm 1965). Describing the habitat use of bats will help to understand the species' habitat needs, and would make it easier for land use planners to determine in which sites and when it could be appropriate to carry out bat surveys. Through the knowledge gathered by this thesis it may be possible to improve the efficiency and quality of bat surveys and their interpretation for appropriate land use planning.

New technologies offer excellent tools for assessing the quality of habitats. Laser scanning provides accurate three-dimensional information through which it is possible to provide virtual reality. This technique can make precise three-dimensional reconstructions of the foraging habitats of bats, e.g. canopy height, density, gap fraction etc. Vegetation structure has been found to be a key component determining habitat quality in birds and research is going on to construct and test habitat quality maps which will make it possible to predict e.g. the distribution and abundance of birds by remote sensing techniques (for a review see Hill et al. 2007). Bats eat insects and forage in places where they exist. Features of echolocation call and wing shape determine the type of habitats in which a bat species can forage (Baagøe 1987). Using the measurements of habitat structures, e.g. vegetation, it is possible to predict the presence of bats. A survey for bats should be indicated when background information suggests that bats may be present and this would be possible with the habitat maps. This technique may also help to improve existing foraging habitats and to create new ones.

Attempts have also been made to characterise bats' winter roosting habitats through three-dimensional data (Addison and Sprouse 2007). To assess the inside quality of hibernacula when bats are not there could also be based on indicators generated from basic studies on bat hibernation requirements. However, the surrounding vegetation and topography around the entrances of hibernacula are important for bats, because they need sheltered flying paths to underground sites (Mitchell-Jones et al. 2007). In this case, airborne information would be useful, e.g. when assessing the quality of hibernacula of long lines of bunkers, such as the Salpa Line, which contains more than 700 installations.

2 MATERIAL AND METHODS

2.1 Study areas

Studies **I**, **II**, **III,** and **VI** were conducted within the temperate coniferous-mixed forest zone in southern Finland (Table 4). The climate of the study area is a mixture of maritime and continental climates. The weather can change quite rapidly, particularly in winter. Summer begins in late May and lasts until mid-September. Winter usually begins during November and ends in late April, the coldest month being February. The average temperature (1971–2000) in the winter is -10– -2 ºC and in the summer 14.1–16.0 ºC. The average precipitation (1971–2000) in the winter is 101–180 mm and in the summer 181–220 mm (Drebs et al. 2002).

Study **V** was carried out in the northern boreal forest zone (Ahti et al. 1968) in northern Finland (Table 4). In northern Finland, summer usually begins in June and ends in August. In the study area, the average temperature (1971–2000) in the winter is -14– -10 ºC and in the summer 12.1–14.0 ºC. The average precipitation (1971–2000) in the winter is 81–120 mm and in the summer 200–220 mm (Drebs et al. 2002). The regions north of the Arctic Circle (66.30^{o} N) are characterised by polar days, when the sun does not set at all. The northernmost parts of Finland have 73 polar days yearly (Drebs et al. 2002).

Study **VII** was conducted in Estonia in the northern part of the mixed forest sub-zone of the temperate forest zone (Estonica 2007; Table 4). The climate of Estonia is a mixture of maritime and continental climates. Special characteristics of Estonian weather are high variability, occasionally strong winds, and high precipitation, as well as abrupt fluctuations in temperature. The average annual temperature is 4.3–6.5 °C and the precipitation 550–800 mm. Winter usually begins during November and ends in late April, the coldest month being February (Estonica 2007). The average temperature in winter (1971–2000) is -3.6 ºC and the average precipitation 131 mm (Eesti Meteoroloogia ja Hüdroloogia Institut 2010).

Data on ambient light levels where bats foraged were gathered in the summer of 2004 (22.6.–19.7.2004) in Finland at 60–67º N.

2.2 Use of foraging habitats

To collect data for studies **II**, **IV**, and **V**, foraging bats were searched for during entire nights. In northern Europe bats forage during the whole night because the nights are very short in summertime (Nyholm 1965; Table 5). Data were not collected in bad weather conditions such as low temperatures, rain, or strong winds, because bats avoid foraging in these conditions.

To detect and identify species, Pettersson D240x and D100 bat detectors were used. The D100 is a heterodyne detector and the D240x has both heterodyne and time expansion functions. A heterodyne detector shifts the ultrasound frequencies downwards so that a human being can hear them. This type of detector offers immediate identification of bats in the field. A heterodyne detector is sensitive only to a limited range of frequencies at any time, so the user selects the ultrasonic frequency range to listen to, just like tuning a radio. To identify the species, the frequency is tuned up and down until the clearest sound is heard.

Table 4. Study areas and timing of studies I–VII in Finland and Estonia.

Study	Core idea	Range of latitudes	Location	Month	Season	Year
I	New hibernating species	60–61ºN and 22–28ºE	Southern Finland	April	Spring	2002
II	Use of foraging habitats	60–62ºN and 22–28ºE	Southern Finland	May–September	Summer	2005
III	Hibernation requirements	60–61ºN and 22–28ºE	Southern Finland	November–April	Winter	2002–2006
IV	Use of foraging habitats Hibernation sites	South of 62ºN	Southern Finland	Throughout the year	All seasons	2002–2006
V	Use of foraging habitats	64º–68ºN	Northern Finland	August–September July-August	Autumn Summer	2005 2006
VI	Hibernation requirements	60–61ºN and 22–24ºE	Southern Finland	November–April	Winter	2003–2005
VII	Hibernation requirements	58–59ºN and 24–25ºE	Estonia	March January	Winter Winter	2005 2006

Table 5. Timing of sunset and sunrise in southern Finland (60º N) and northern Finland (65º N and 69º N) in May, June, July, August and September (The Almanac Office at the University of Helsinki 2010).

	Southern Finland Helsinki (60º N)		Northern Finland Oulu (65º N)		Northern Finland Utsjoki (69º N)	
	Sunset	Sunrise	Sunset	Sunrise	Sunset	Sunrise
May	21.18–22.25	5.18–4.11	21.55–23.31	4.45–3.03	22.36–	3.46–
June	22.29–22.48	4.08–3.59	23.38–0.14	2.57–2.29	–	–
July	22.47–21.55	4.00–4.75	0.12–22.35	2.31–4.11	–0.06	–2.32
August	21.52–20.28	4.59–6.12	22.32–20.41	4.14–5.53	23.48–20.59	2.41–5.23
September	20.25–18.56	6.14–7.23	20.38–18.51	5.56–7.24	20.54–18.40	5.25–7.22

A time expansion detector first stores a portion of the ultrasonic signal in its digital memory and then replays it at a slower speed. The entire ultrasonic range is audible all the time. The output can be recorded for later analysis. In unclear cases, the recorded sounds were analysed with the sound analysing program BatSound Pro 3.3 (Pettersson Elektronik Ab 2004). Call parameters such as the highest and lowest frequency, the frequency of main energy, and the duration of the signal can then be analysed from sonograms for identification of the species (Table 6).

When two persons were together in the field one used the Pettersson D240x and the other the D100, because the D100 has more sensitive microphones, i.e. it detects bats' voices better. When only one person was doing the field work he/she often used a D240x tailored to continuously scan and play 0.1-second time-expansion sounds. Bats were also detected by placing two bat detectors on the roof of a Land Rover, a Pettersson D240x, tailored to continuously scan and play 0.1-second time-expansion sounds, and a Pettersson

Table 6. Echolocation call parameters of the six bat species (Obrist et al. 2004) studied in Finland.

	Brandt's bat/ whiskered bat	Daubenton's bat	Natterer's bat	Northern bat	Brown long-eared bat
Call duration (ms)	3.6 ± 0.5	3.9 ± 0.9	4.1 ± 1.1	10.7 ± 1.6	2.9 ± 0.6
Frequency of maximum energy (kHz)	46.8 ± 5.6	42.7 ± 3.5	40.4 ± 8.8	29.8 ± 1.6	37.7 ± 5.1
Minimum frequency (kHz)	27.9 ± 3.5	27.3 ± 3.0	14.0 ± 4.0	24.6 ± 1.1	22.7 ± 1.7
Maximum frequency (kHz)	99.7 ± 12.6	81.2 ± 8.0	108.6 ± 18.6	48.2 ± 8.8	55.7 ± 5.6

D100 heterodyne detector tuned to the frequency of 35 kHz so that both heterodyne and time expansion sounds could be heard at the same time inside the vehicle. The advantage of a heterodyne detector is that it works in real time, while a time expansion detector samples bat calls intermittently. When the recorded sample is being played back slowly, nothing is being recorded. To avoid long pauses in the detection of bats, the D240x was tailored to continuously scan and play 0.1-second time-expansion sounds.

The signal stored in the time expansion memory of the Pettersson D240x detector can be replayed at its original speed (in heterodyne form) through heterodyne systems, which made it possible for us to perform a careful examination of the signal's main frequency in the field. Sonograms were also analysed in the field with the sound analysing program BatSound Pro 3.3 with a DAQCard-6062E from National Instruments with a portable computer. Summer nights are bright in northern Europe (Figure 1, Table 5), which makes it possible to count the number of bats, and to observe the behaviour and characteristics of bats to confirm the identification of the species.

The echolocation calls (heterodyne and time expansion) of the northern bat are quite easy to identify. Its voice is so loud that it can be heard at least 50 m away (Ahlén 1981).

There is a great variation from pulse to pulse in the echolocation calls of the brown long-eared bat. The echolocation calls of this species can be so weak that they are heard only at a distance of less than 5 m. Sometimes this species emits loud calls at an irregular rate that can be heard at least 40 m away. This species is often silent, because when gleaning it does not usually use echolocation to search for food but listens to the noise generated by its prey. When it is silent it can be identified by visual observations, because this species typically hovers or circles around trees and bushes (Ahlén 1981). Because the brown long-eared bat is often silent, it might be underestimated in this study.

Myotis species are more difficult to distinguish from each other (Ahlén 1981). The echolocation calls of Brandt's bats and whiskered bats are so similar that it is not possible to distinguish them from each other by their sounds. The echolocation calls of Brandt's bats/whiskered bats are difficult to distinguish from those of Daubenton's bats when both species are foraging in the same habitat, i.e. in a forest. When hunting over water, Daubenton's bat has a special hunting technique of circling around close to the water

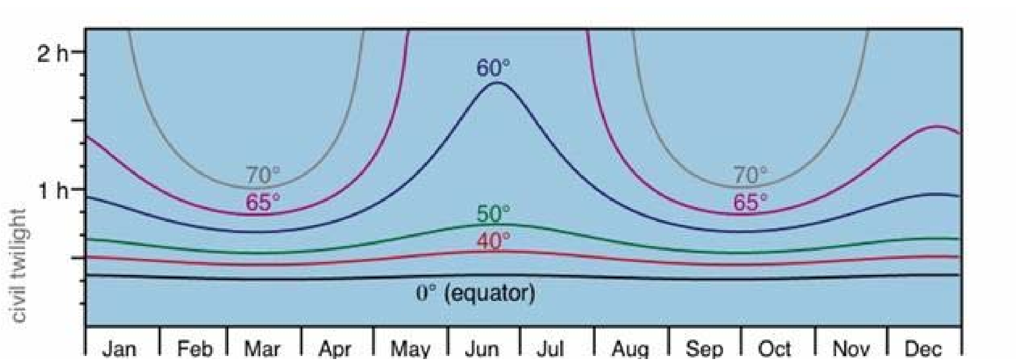


Figure 1(© Hannu Karttunen). Length (h) of civil twilight at different latitudes and time of the year. Twilight is the time between dawn and sunrise, and between sunset and dusk. It can be described as the limit at which the ambient light level is sufficient for terrestrial objects to be clearly distinguished (Naval Oceanography Portal 2010).

surface. The sounds of Natterer's bats are often weaker than those of Brandt's bats/whiskered bats and Daubenton's bats and their repetition rate is higher. Natterer's bats typically fly around in a small space, so visual observations can help the identification of this species. This species often inspects a human being by circling around in front of him/her (Ahlén 1981). Natterer's bat also emits loud long-sweep sounds like the brown long-eared bat. However, these types of sounds are softer in the brown long-eared bat (Ahlén 1981).

For study **II** different types of habitats were searched according to their occurrence in the region. For study **V**, Daubenton's bat in particular was searched for by stopping on all bridges and river banks to listen with bat detectors, and particularly investigating river valleys. When commuting from one body of water to another, other bat species were also searched for.

Whenever a bat was observed, the species and characteristics of the habitat where the bat foraged were recorded. In study **V**, the width of the river was recorded if a bat foraged on a river.

Ambient light levels (lux) where northern bats, Daubenton's bats, and Brandt's/whiskered bats foraged were measured using a Delta OHM HD 9221 photometer. Whenever a bat was observed to forage at 1.0 lux or at higher ambient light level values, the values were recorded.

2.3 Hibernation requirements

The numbers of hibernacula surveyed for study **III** are presented in Table 7. One hibernaculum studied was a tunnel of an abandoned mine, and all the other hibernacula were military constructions. All the hibernacula had multiple entrances at different elevations. Twelve per cent of the hibernacula surveyed were completely concrete constructions, whereas the remaining 88% were combinations of natural rock and concrete.

Table 8 presents detailed features of the hibernacula surveyed for study **VI**. Hibernacula 1–7 were surveyed in winter 2003/2004, and hibernacula 1–5 and 7–9 in winter 2004/2005. All the hibernacula were Salpa Line military constructions located less than 5 km from each other. The surrounding area was mainly mixed woodland, but there were also farms and houses nearby. All the hibernacula were located less than 5 km from the Gulf of Finland, approximately 30 m above sea level. The hibernacula were at a depth of 5–10 m. Their height was 2–3 m and they had 2–4 entrances. The entrance area was defined as the first 0–10 m from the mouth of the hibernacula. The length of the passages varied from 34–73 m, and the total surface area of the roof and walls was 290–660 m^2.

According to Dallas Semiconductor temperature loggers placed in the middle of the chambers (or in the middle of the hibernacula without chambers) of every underground site, the temperatures inside all the hibernacula roughly followed the fluctuations of the outside air temperature recorded at a meteorological station approximately 10 km away (Figure 2).

For study **VII** seven hibernacula were surveyed in Estonia in 2005. These were the abandoned Ülgase mine, four abandoned limestone cellars (three cellars in Järvikandi and one in Haimre), and two military constructions, one with natural stone walls in Väänäposti and the other with concrete walls in Viti. Eight hibernacula were surveyed in 2006. These were the abandoned Ülgase mine, four abandoned limestone cellars (three cellars in

Table 7. Number of hibernacula that housed bats in studies I, III, IV, VI, and VII in Finland and in Estonia.

Study	Core idea		Number of hibernacula with bats
I	Hibernating new species in Finland		1
III	Hibernation requirements of bats in southern Finland		
		winter 2002/2003	35
		winter 2003/2004	76
		winter 2004/2005	108
		winter 2005/2006	25
IV	Hibernation sites of Natterer's bat in Finland		
		winter 2001/2002	1
		winter 2003/2004	4
		winter 2004/2005	5
		winter 2005/2006	4
VI	Seasonal hibernation requirements of bats in Finland		
		winter 2003/2004	7
		winter 2004/2005	8
VII	Hibernation requirements in Estonia		
		winter 2004/2005	7
		winter 2005/2006	8

Järvikandi and one in Haimre), and three military constructions, two with natural stone walls in Humala and Väänäposti and one with concrete walls in Viti. The mine and military constructions had back sections (rear wings) with stable conditions and a higher temperature, whereas in the front sections, the temperature was lower and more variable, fluctuating according to the climatic conditions outside the underground site. The cellars had no back parts with more stable conditions, but their temperature fluctuated according to the climatic conditions outside them.

To collect data for studies **I**, **III**, **IV**, **VI**, and **VII,** hibernating bats were searched for in underground hibernacula (Table 7). A self-standing ladder was used to investigate bats high on the wall or ceiling. For data analysis a record was made of whether the bat hibernated solitarily or clustered (including the size of the cluster) and whether the bat hibernated on the wall/ceiling or in a crevice. All the holes that a bat can enter completely were classified as crevices. Most crevices were 5–20 cm long, the maximum being 50 cm, and their width was 2–20 cm. Bats that were in body contact with each other were classified as clustered. The temperature and relative humidity were measured within 5 cm of the bat, using two

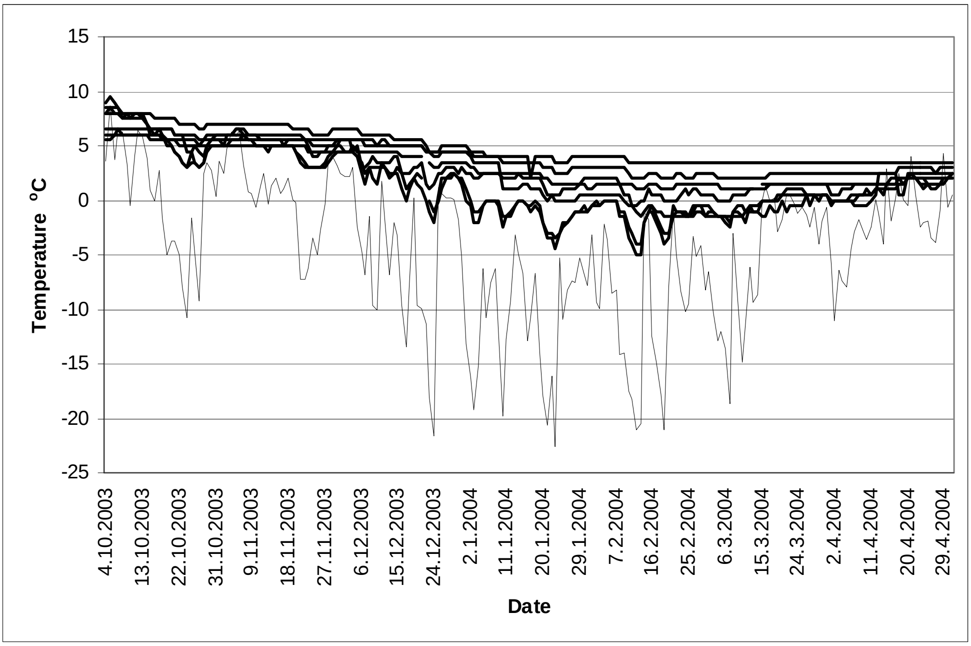
Table 8. Features of the nine hibernacula surveyed for bats in the Salpa Line region of Finland in the winters of 2003/2004 and 2004/2005 (*one entrance with stairs).

		Type of entrances							
Hibernacula	Number of entrances	Doorway	Porthole	Lookout tower	Wide opening under construction	Number of chambers	Width and length of chambers (m x m)	Length of passages (m)	Surface of roof and walls (m^2)
1	2	1	1	-	-	1	4 x 25	42	414
2	4	2	-	1	1	0	-	64	641
3	4	2*	2	-	-	1	4 x 10	73	561
4	3	1	1	1	-	1	4 x 10	50	379
5	2	2	-	-	-	0	-	32	302
6	3	1*	1	1	-	1	2 x 14	51	336
7	3	-	-	-	3	0	-	55	660
8	3	1*	2	-	-	1	5 x 15	29	291
9	3	1*	1	1	-	1	5 x 15	34	325

humidity and temperature meters: a VAISALA HM 34 and a VAISALA HMI 41 with a HMP 44L probe (2.7 m; VAISALA, Vantaa Finland), which provide fast and accurate results. The measurement range of both meters for humidity is 0–100% (0–90% ±2%, 90–100% ± 3%) and for temperature -20–60°C (± 0.3 °C).

To identify the species we used a Sony DSC-F828 digital camera, a SnakeEye video inspection system (Panametrics-NDT, Waltham, U.S.A.), Swarovski EL 10x32 binoculars, a two-sided dentist's mirror, and a make-up mirror with a 1.5-metre handle. The mirror pivoted in such a way that a crevice could be inspected from different angles. With this equipment it was possible to thoroughly investigate most of the crevices for bats.

For study **VII**, the locations of bats were recorded on maps (roof and walls) of the hibernacula. In addition, the temperature and humidity were measured at a height of 2 m



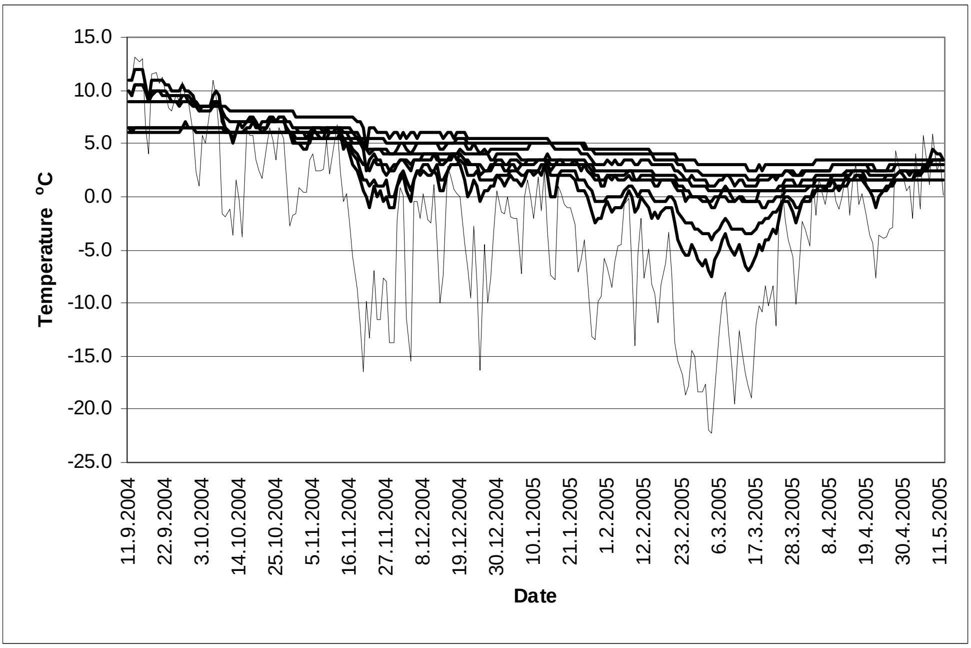


Figure 2. The relation of outdoor temperature (thin line) to the temperature inside the underground site (thick line) measured in hibernacula in the Salpa Line, Finland, in the winter of 2003/2004 (seven hibernacula) and in the winter of 2004/2005 (eight hibernacula).

with a VAISALA HM 34 at every 5 m along passages to determine changes in them during different portions of the season of hibernation. The water vapour pressure difference determines the direction and rate of the movement of water vapour, so the water vapour pressure was calculated from relative humidity and temperature, e.g. Louw (1993) for data analyses.

2.4 Identification of Brandt's bat and the whiskered bat

Brandt's bat and the whiskered bat resemble each other very closely and cannot be separated in the field without handling them. Therefore these two species are presented together as Brandt's/whiskered bats.

2.5 Data analysis

SPSS 14.0 and 16.0 for Windows (SPSS Inc. 1989–2006) were used to analyse the data. A p-value of <0.05 was considered significant. Throughout, a non-parametric equivalent of analysis of variance, the Kruskal-Wallis analysis of ranks, was used to compare the differences between groups, because the data were not normally distributed. Analyses of frequencies were made using χ^2-tests throughout. The Mann Whitney U-test was used to compare the Estonian data between the years 2005 and 2006, and the use of temperatures in crevices and outside crevices within species. The diversities of foraging habitats used by different species were determined by using the complement of the Simpson's index of diversity (Magurran 2007):

$$D = 1 - \sum_{p=i}^{N} p_i^2 \tag{1}$$

where p is the proportion of individuals in a habitat type and N is the number of habitat types. In this study, the index of diversity presents the probability that if two individuals are randomly chosen they will forage in different habitats.

3 RESULTS

3.1 Occurrence of bat species (I–VII)

The same seven species were found to hibernate both in Finland and in Estonia (Table 9). The most commonly detected species in southern Finland, both in summer and winter, was Brandt's/whiskered bats, whereas in northern Finland the northern bat was the most commonly detected species (Table 9). The pond bat was found for the first time in Finland

Table 9. Number of observations of bats in studies I–VII in Finland and in Estonia.

Study	Core idea	Number of observations Brandt's bat/ whiskered bat	Pond bat	Daubenton's bat	Natterer's bat	Northern bat	Brown long-eared bat
I	Hibernating new species		1				
II	Foraging habitats in southern Finland	1196		412		902	38
III	Hibernation requirements in southern Finland	2093		425		733	138
IV	Natterer's bat						
	Foraging habitats				7		
	Hibernation sites				20		
V	Foraging habitats in northern Finland	3		75		202	6
VI	Seasonal hibernation requirements						
	beginnig of the season	550		72		69	22
	mid-season	787		81		216	44
	end of the season	495		65		113	12
VII	Hibernation requirements in Estonia						
	2006	100	150	252	34	195	69
	2005	88	74	65	23	116	48

in March 2002. The northern bat, Brandt's/whiskered bats, Daubenton's bat, and the brown long-eared bat occurred both in southern and northern Finland, whereas the pond bat and Natterer's bat occurred only in southern Finland.

The northernmost Daubenton's bat was found above 66° N. No Daubenton's bat was found between 65° N and 66° N. The northernmost Brandt's/whiskered bats occurred above 66° N, and the northernmost brown long-eared bat above 64° N.

3.2 Use of foraging habitats (II, IV, V)

In southern Finland (below 62° N), Brandt's/whiskered bats and brown long-eared bats foraged mainly in forest habitats, including forest edges, whereas Daubenton's bats foraged mainly in water habitats, including water edges (Table 10). Natterer's bats foraged in edge

Table 10. Percentages in the use of foraging habitats by bat species in southern and northern Finland in studies II, IV, and V.

	Southern Finland					Northern Finland			
Habitat	Brandt's bat/ whiskered bat	Daubenton's bat	Natterer's bat	Northern bat	Brown long-eared bat	Brandt's bat/ whiskered bat	Daubenton's bat	Northern bat	Brown long-eared bat
Open water	0.5	43.0	-	6.7	-	-	2.7	3.0	-
Linear water	1.0	37.6	-	11.5	2.6	-	95.9	50.5	-
Shore with vegetation edge	0.2	3.4	-	3.7	5.2	-	1.4	0.5	16.7
Shore without vegetation edge	0.3	3.4	-	4.2	-	-	-	-	-
Harbour	0.1	3.4	-	1.1	-	-	-	-	-
Bridge	-	2.9	-	0.4	-	-	-	5.0	-
Grassland	1.0	-	-	2.4	8.0	-	-	1.0	-
Urban area	1.7	1.0	-	13.7	2.6	-	-	13.0	-
Park	1.2	1.7	-	6.0	15.8	-	-	5.9	83.3
Road	-	1.0	-	3.8	-	-	-	5.0	-
Other treeless areas	-	-	-	0.6	-	-	-	1.5	-
Rural area	5.6	0.5	-	3.5	-	-	-	5.0	-
Stand of sapling or bushes; clear cut	0.1	-	-	1.0	2.6	-	-	-	-
Deciduous woodland	4.0	0.5	-	0.8	26.3	-	-	-	-
Mixed woodland	20.2	0.5	-	2.4	10.5	100.0	-	0.5	-
Coniferous woodland	53.1	0.5	-	11.4	10.5		-	3.0	-
Deciduous woodland edge	0.2	0.5	42.9	3.1	5.3	-	-	2.0	-
Mixed woodland edge	2.7	0.2	-	9.5	5.3	-	-	2.0	-
Coniferous woodland edge	8.4	0.2	-	13.7	5.3	-	-	1.5	-
Edge of a park	-	0.2	57.1	0.4	-	-	-	0.5	-
Index of diversity in habitat use	0.66	0.67	-	0.91	0.86	-	0.08	0.75	-

habitats (deciduous forests and meadows/fields). Northern bats used foraging sites opportunistically and the index of diversity in habitat use of this species was higher than in the other species (Table 10). However, above 64º N, its diversity in habitat use was lower than in southern Finland.

When foraging in woodland, northern bats typically hunted in clearings and above forests. The forests where Brandt's/whiskered bats foraged were not dense, and the species hunted between trees, as well as above small openings and paths in the middle of the forests. Daubenton's bats typically foraged in low searching flight above water surfaces (trawling) and seldom caught insects high in the air over an aquatic habitat. This species foraged on water without plant growth on the surface. During light summer nights, the species preferred to hunt on the shadiest side of bodies of water, e.g. the north/north-eastern shores of lakes. During windy nights it often hunted in thin forests near bodies of water.

Above 64º N, Daubenton's bats foraged almost exclusively on rivers (Table 10). The northernmost Daubenton's bats foraged over quiet waters just below rapids in the deep river valleys of the Koutajoki catchment area, which flows to the White Sea in Russia.

Fifty per cent of northern bats and Daubenton's bats foraged over linear landscape features, whereas Brandt's/whiskered bats and brown long-eared bats typically used non-linear foraging sites.

All species foraged both solitarily and together with other bats. Although the majority of bats foraged together with other bats, they were never observed to defend their foraging sites aggressively. Occasionally, foraging northern bats and Daubenton's bats were observed to interact (playing) with conspecifics.

In southern Finland, northern bats and brown long-eared bats typically foraged alone in the locations that were studied, whereas Brandt's/whiskered bats typically foraged together with conspecifics (Table 11). In northern Finland, Daubenton's bats typically foraged in multispecies locations (Table 11). In northern Finland, only two species were found to forage together. In southern Finland, three species were found to forage together in three locations, but at other multispecies foraging sites only two species foraged together. The most common multispecies compositions at a foraging site both in southern and northern Finland were northern bats and Daubenton's bats. The most common multispecies foraging habitat both in southern and northern Finland was linear water (rivers, canals, and streams).

Table 11. The percentages of locations where bats foraged alone, together with their conspecifics or, together with other species in northern and southern Finland.

	Alone	With conspecifics	With other species	
Southern Finland				
Brandt's/whiskered bat	27%	57%	16%	100% (N=328)
Daubenton's bat	32%	35%	33%	100% (N=190)
Northern bat	52%	26%	22%	100% (N=532)
Brown long-eared bat	52%	7%	41%	100% (N=29)
Northern Finland				
Brandt's/whiskered bat	100%	0%	0%	100% (N=3)
Daubenton's bat	19%	23%	58%	100% (N=26)
Northern bat	38%	37%	25%	100% (N=68)
Brown long-eared bat	0%	50%	50%	100% (N=2)

Northern bats (N = 87, 21.8 ± 58.0 lux) tolerated higher ambient light levels (max 356 lux), whereas Brandt's/whiskered bats (N = 44, 1.4 ± 0.4 lux) were observed to forage when the ambient light levels were lower than 3 lux and Daubenton's bats (N = 30, 2.6 ± 6.0 lux) when they were lower than 35 lux. Two northern bats foraged with three barn swallows (*Hirundo rustica*, Linnaeus, 1758) over a road at 59.8 lux in Haapajärvi (25º20'E, 63º45'N).

3.3 Hibernation requirements (III, IV, VII)

Both in southern Finland and in Estonia, among the northern bat, Brandt's/whiskered bats, Daubenton's bat, and the brown long-eared bat, the northern bat and the brown long-eared bat hibernated in colder and drier locations, whereas Daubenton's bat and Brandt's/whiskered bats hibernated in warmer and more humid locations (Table 12). In Estonia, Natterer's bat used lower temperatures and humidity for hibernation than other species, whereas the temperatures and humidity used by the pond bat were higher than those used by other species. All species hibernated both solitarily and in small clusters of up to 13 individuals in Finland and up to 25 in Estonia. Northern bats, brown long-eared bats, Daubenton's bat, and Natterer's bat typically hibernated solitarily. In Finland, Brandt's/whiskered bats and, in Estonia, pond bats typically used clusters. Brandt's/whiskered bats, brown long-eared bats, and Natterer's bats typically used crevices for hibernation. Bats typically used crevices in colder and drier locations and hibernated on the wall/ceiling in warmer and more humid locations (Table 13a and b).

Daubenton's bats typically hibernated on the wall/ceiling in Finland. Brandt's/whiskered bats used narrow cracks where they could have body contact with walls on all sides. Like Brandt's/whiskered bats, the brown long-eared bat typically used crevices, but it was not necessary for it to have body contact with the substrate on all sides. The brown long-eared bat often entered large crevices, where it could hang from the crevice ceiling by its hind feet without having any other contact with the substrate. In Estonia, all clusters were composed of one or two species, whereas in Finland one cluster with three species was also found. Both in Estonia and Finland the brown long-eared bat was never found to use the same clusters as Daubenton's bat, and Natterer's bat was found to cluster only with the Northern bat and the brown long-eared bat. In Estonia, the pond bat clustered with Brandt's/whiskered bats and Daubenton's bat. Natterer's bats were found to hibernate only in limestone cellars, whereas pond bats never hibernated there.

In Finland, Brandt's/whiskered bats and Natterer's bats hibernated only on/in natural rock, while 15% of northern bats, 1% of Daubenton's bats and 1% of brown long-eared bats hibernated on/in concrete substrate. In addition, northern bats were found inside iron constructions three times.

The Estonian hibernacula housed approximately 77 ± 104 bats, whereas the Finnish hibernacula housed approximately 14 ± 18 bats and only one hibernaculum housed over 100 bats (N=121).

3.4 Seasonal variation in hibernation requirements (VI)

The hibernacula were coldest in the middle of the hibernation season and warmest at its beginning, whereas the humidity was at its highest at the beginning of the season and

Table 12. Environmental measurements, clustering, and location of bats in Estonian and Finnish hibernacula. Temperature indicates the temperature at which a bat hibernated. Water vapour pressure indicates the humidity at which a bat hibernated. Solitary hibernation indicates the proportion of bats that hibernated solitarily. Crevice occupation indicates the proportion of bats that hibernated in crevices.

	Northern bat	Brandt's bat/ whiskered bat	Daubenton's bat	Brown long-eared bat	Natterer's bat	Pond bat
Temperature (x ± SD)						
Estonia 2005	4.1 ± 1.5 ºC	5.9 ± 0.8 ºC	4.8 ± 1.6 ºC	3.8 ± 1.7 ºC	2.7 ± 0.5 ºC	6.8 ± 0.9 ºC
Estonia 2006	4.3 ± 2.0 ºC	6.0 ± 1.1 ºC	6.5 ± 1.7 ºC	4.6 ± 1.7 ºC	3.4 ± 0.8 ºC	7.1 ± 1.2 ºC
Southern Finland	2.0 ± 2.5 ºC	4.0 ± 2.1 ºC	4.4 ± 2.7 ºC	2.7 ± 2.3 ºC	-	-
Water Vapour Pressure (x ± SD)						
Estonia 2005	749 ± 105 Pa	870 ± 59 Pa	799 ± 104 Pa	723 ± 126 Pa	653 ± 41 Pa	935 ± 89 Pa
Estonia 2006	751 ± 116 Pa	876 ± 82 Pa	923 ± 131 Pa	783 ± 112 Pa	737 ± 49 Pa	960 ± 97 Pa
Southern Finland	565 ± 117 Pa	705 ±129 Pa	756 ± 197 Pa	636 ± 152 Pa	-	-
Solitary hibernation						
Estonia 2005	90%	49%	89%	94%	83%	36%
Estonia 2006	74%	38%	86%	100%	79%	43%
Southern Finland	64%	30%	80%	72%	70%	-
Crevice occupation						
Estonia 2005	35%	74%	49%	58%	100%	69%
Estonia 2006	39%	71%	45%	68%	100%	44%
Southern Finland	54%	84%	30%	74%	100%	-

Table 13a. Comparison of temperatures (ºC) used by bats inside and outside crevices in Estonia and in Finland.

		Northern bat	Brandt's bat/ whiskered bat	Daubenton's bat	Brown long-eared bat	Natterer's bat	Pond bat
Estonia 2005							
	On the wall/ceiling	4.6 ± 1.1	5.9 ± 1.0	5.4 ± 1.1	4.6 ± 1.5	-	6.9 ± 0.8
	In crevises	3.2 ± 1.7	5.9 ± 0.7	4.2 ± 1.8	3.2 ± 1.7	2.7 ± 0.5	6.7 ± 1.0
Estonia 2006							
	On the wall/ceiling	5.0 ± 1.4	6.5 ± 1.1	7.0 ± 1.3	5.9 ± 1.4	-	7.6 ± 0.9
	In crevises	3.2 ± 2.3	5.9 ± 1.1	5.9 ± 2.0	4.0 ± 1.4	3.4 ± 0.8	6.4 ± 1.2
Finland							
	On the wall/ceiling	2.4 ± 2.5	4.7 ± 2.0	4.9 ± 2.7	3.8 ± 2.0	-	-
	In crevises	1.7 ± 2.5	3.8 ± 2.1	3.3 ± 2.5	2.4 ± 2.3	-	-

Table 13b. Comparison of water vapour pressures (Pa) used by bats inside and outside crevices in Estonia and in Finland.

		Northern bat	Brandt's bat/ whiskered bat	Daubenton's bat	Brown long-eared bat	Natterer's bat	Pond bat
Estonia 2005							
	On the wall/ceiling	789 ± 34	901 ± 79	840 ± 74	778 ± 118	-	977 ± 63
	In crevises	674 ± 115	859 ± 47	756 ± 113	683 ± 119	653 ± 41	916 ± 93
Estonia 2006							
	On the wall/ceiling	786 ± 89	909 ± 79	962 ± 103	871 ± 111	-	1013 ± 68
	In crevises	697 ± 131	863 ± 80	877 ± 146	742 ± 86	737 ± 49	892 ± 86
Finland							
	On the wall/ceiling	579 ± 182	764 ± 125	794 ± 198	691 ± 160	-	-
	In crevises	554 ± 172	695 ± 127	665 ± 161	616 ± 146	-	-

Table 14. Summary of microclimatic measurements taken at a height of 2 m every 5 m along passages of nine hibernacula surveyed for bats in the Salpa Line region of Finland during different periods of the hibernation season in the winters of 2003/2004 and 2004/2005.

	Portion of the season		
	Beginning	Mid	End
N	367	504	378
Temperature (ºC)			
Mean	5.3	2.0	2.7
SD	2.8	2.0	2.3
Minimum	-5.3	-3.2	-5.0
Maximum	10.2	7.3	12.8
Water vapour pressure (Pa)			
Mean	839	654	638
SD	165	118	115
Minimum	327	382	239
Maximum	1174	943	781

similar between the middle and end of the hibernation season (Table 14). The chambers (posterior parts) had more stable conditions than the anterior parts of the hibernacula. Mean temperatures and water vapour pressures were higher in the chambers throughout the season (Table 15).

Brandt's/whiskered bats were observed in the hibernacula from October till May, Daubenton's bats from October till April, northern bats from November till April, and brown long-eared bats from October till April in the winter of 2003/2004 and from November till March in the winter of 2004/2005. The numbers of bats in the hibernacula were highest in the middle of the hibernation season (Table 9).

At the beginning of the season all species used more humid and warmer conditions than at the end of the season (Table 16).

Clustering increased towards the end of the season in all species. More than 50% of northern bats, Daubenton's bats, and brown long-eared bats hibernated solitarily in all seasons, whereas most Brandt's/whiskered bats hibernated in clusters (Table 16).

More Brandt's/whiskered bats used crevices towards the end of the hibernation season. More crevice bats stayed in clusters at the end of the season than at the beginning of the season in the northern bat, Brandt's bats/whiskered bats, and Daubenton's bats.

Towards the end of the season of hibernation greater numbers of Brandt's/whiskered bats hibernated in chambers, on the ceiling and in the highest parts of the hibernacula.

Table 15. Summary of ambient water vapour pressures (Pa) and temperatures (ºC) for all bat locations and hibernacula passages measured in nine hibernacula in the Salpa Line, Finland, during different periods of the bat hibernation season in the winters of 2003/2004 and 2004/2005.

Portion of the season			Water vapour pressure (Pa)				Temperature (ºC)			
		N	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Beginning	Entrance	229	316	1219	780	194	-5.3	10.3	4.6	3.6
	Corridor	404	427	1129	815	156	-1.7	10.3	5.2	2.5
	Chamber	456	624	1114	917	86	2.1	10.4	6.9	1.2
Mid	Entrance	309	353	877	601	116	-4.1	8.7	1.4	2.2
	Corridor	563	449	1090	650	97	-1.7	8.1	2.2	1.6
	Chamber	760	527	1002	794	81	0.7	10.1	5.2	1.6
End	Entrance	216	239	881	639	120	-5.3	12.8	3.1	2.9
	Corridor	288	234	800	624	127	-3.3	6.9	2.4	2.1
	Chamber	654	355	848	711	68	-0.4	6.7	4.2	1.7

Table 16. Environmental measurements, clustering, and location of bats in nine hibernacula in the Salpa Line, Finland, during different periods of the bat hibernation season in the winters 2003/2004 and 2004/2005.

		Northern bat	Brandt's bat/ whiskered bat	Daubenton's bat	Brown long-eared bat
Temperature (ºC)					
	Beginning	3.7 ±3 .3	6.2 ± 2.0	6.5 ± 2.6	5.8 ± 2.8
	Mid	2.7 ± 2.4	4.5 ± 2.2	4.0 ± 1.6	3.2 ± 2.0
	End	2.4 ± 2.2	4.2 ± 2.0	3.7 ± 1.8	3.4 ± 1.2
Water vapour pressure (Pa)					
	Beginning	741 ± 184	867 ± 130	896 ± 156	846 ± 177
	Mid	666 ± 139	750 ± 111	744 ± 91	696 ± 128
	End	621 ± 146	710 ± 72	690 ± 94	656 ± 74
Solitary hibernation					
	Beginning	91%	47%	92%	96%
	Mid	58%	32%	75%	77%
	End	64%	26%	57%	83%
Crevice occupation					
	Beginning	54%	79%	49%	64%
	Mid	63%	83%	33%	72%
	End	61%	92%	68%	75%
Hibernation on the ceiling					
	Beginning	64%	48%	67%	50%
	Mid	60%	64%	74%	43%
	End	54%	70%	67%	50%
Hibernation in chambers					
	Beginning	27%	52%	38%	32%
	Mid	27%	62%	57%	21%
	End	22%	76%	35%	50%

4 DISCUSSION

4.1 Use of foraging areas

In northern Europe, the brightness of summer nights may be an important factor that restricts the habitat use of Daubenton's bats and Brandt's/whiskered bats. Bats usually fly and feed in the darkness, but in northern Europe they are forced to forage during bright midsummer nights. The predation risk is higher at higher ambient light levels. The risk of being caught by visually oriented predators and diurnal birds, such as hawks and falcons, decreases with a decreasing light level (Speakman 1991, 1995, Rydell and Speakman 1995, Rydell et al. 1996). It is probably more difficult for predators to catch fast-flying bat species and consequently they tolerate higher ambient light levels.

The length of civil twilight during summer increases towards the north in the northern hemisphere. In this study, northern bats tolerated higher ambient light levels than did Daubenton's bats and Brandt's/whiskered bats. The bright summer nights may restrict the distribution of Daubenton's bats and Brandt's/whiskered bats towards the north, because dark hunting places are difficult to find in northern Finland. In habitat use both species were more selective than the northern bat and the brown long-eared bat, Daubenton's bat foraging almost exclusively in water habitats and Brandt's/whiskered bats in forest habitats. In northern Finland the forests are lighter than in the south, because the tree stands are sparse and low, which may restrict the possibility of Brandt's/whiskered bats hunting there. In the Koutajoki catchment area, where the northernmost Brandt's/whiskered bats were found, they all hunted in tall forests. In this area the conditions are favourable and tall forests exist.

Daubenton's bat avoids open areas before full darkness (Nyholm 1965). In northern Finland, Daubenton's bat foraged almost exclusively on rivers, probably because they are duskier foraging areas than lakes. In the Kuusamo region, however, there are noticeable differences in elevations, e.g. deep canyons and cliffs in woodland. The cliffs, canyon walls, and tall forests shaded the surface of the rivers where Daubenton's bat hunted, offering shaded flight paths and hunting places for this species. The northern bat occurs up to 70^{o} N in Fennoscandia and typically forages in valleys (Speakman et al. 2000) and canyons (Iso-Iivari 1988) in the northernmost part of its distribution. Similar to Rydell (1989), the northern bat foraged over lakes and other open areas to a minor extent in northern Finland.

The occurrence of Daubenton's bat and Brandt's/whiskered bats in the Koutajoki catchment area suggests that the warmth of the summers may be an important factor for the distribution of these species. In the Torniojoki river valley, which is the national border between Finland and Sweden, a lot of suitable habitats for Daubenton's bat exist, but no individuals have been found so far. The climatic conditions in the valley are as mild as in central Finland, although it is situated in the Arctic Circle, between 65^{o}45' N and 67^{o}15' N. The lack of dusky flying paths may prevent Daubenton's bat from expanding its distribution to the Tornio River Valley. In western Finland, lakes are scarce and all the rivers flow from the south-east to the north-west. Thus no flying paths exist for this species to commute from one river to another. Moreover, the species cannot follow the coastline of the Gulf of Bothnia, because it avoids open habitats during light summer nights and flies only in dusky places.

Daubenton's bats were not found between 65^{o} N and 66^{o} N in eastern Finland. When commuting and foraging, Daubenton's bat often follows the edges of bodies of water, and in the vicinity of the border of its distribution it prefers to fly along dusky rivers in forested areas. Therefore, it may face difficulties in passing the watershed area, because there are no shaded flying paths for it towards the north.

In northern Finland, Daubenton's bats typically foraged together with northern bats. This may be one strategy to reduce the risk of predation (e.g. avoiding detection, diluting individual risk, confusing predators, and early detection; for a review see Barnard 2004) at high ambient light levels or different species may simply gather to forage together in shady places or sites with an aggregation of insects. Insects are patchily distributed and more bats may simply gather to forage together because there is plenty of food and vice versa, i.e. bats forage alone when the insect density is not high.

The northern bat was observed to forage together with barn swallows. The northern bat forages together with other bat species (e.g. Haupt et al. 2006), but this is the first time that northern bats were observed to forage together with birds. This contrasts with the findings of Speakman et al. (2000), who never observed this species foraging together with birds and suggest that in Northern Norway it avoids feeding competition with insectivorous birds.

4.2 Foraging areas – implications for land use planning

The index of diversity in habitat use was high in the northern bat, both in southern and northern Finland, suggesting that it was opportunistic all over Finland, foraging in a wide range of habitats, thus corroborating Rydell (1992a), and Haupt et al. (2006). In northern Finland, data on northern bats were gathered when searching for Daubenton's bat and this may affect the results, i.e. causing a lower index of diversity.

This study indicates that northern bats and brown long-eared bats are more tolerant of changes in their environment; because their indices of diversities in the use of foraging habitats were high, they tended to disperse to a large number of foraging sites, and both species typically foraged in man-made environments: the northern bat in urban areas and the brown long-eared bat in parks.

Brandt's/whiskered bats tended to gather to forage together with conspecifics in suitable forests, and these foraging areas should be conserved through land use planning when possible. Although woodland covers 68% of the total area of Finland (Statistics Finland 2005), suitable habitats should be conserved and maintained for Brandt's/whiskered bats; in urban areas the habitats of these species are threatened by the construction of new buildings and in the countryside by intensive forestry. Large clear cuts should be avoided in the foraging habitats of Brandt's/whiskered bats. Conversely, to maintain local foraging habitats for these species, the thinning of dense forests, both young and old, is needed so that the species have enough space to fly and hunt insects. In addition, small clearings could be created here and there in the middle of the forests. In southern Finland, Brandt's/whiskered bats were detected more often than northern bats in both the summer and winter, suggesting that one of these species or both of them are very common in southern Finland.

Brandt's/whiskered bats, Natterer's bat, the northern bat and the brown long-eared bat foraged mainly on forest habitats and Daubenton's bat on water bodies typically near protective tree stands. All these species use trees for roosting (e.g. Mitchell-Jones et al. 1999). According to Section 14 b (Procedure for declaration concerning flying squirrels; 552/2004) of the Finnish Forest Act (1093/1996; amendments up to 552/2004 included), "if a forest use declaration received by the Forestry Centre concerns a breeding and resting site of flying squirrels referred to in a document delivered by the Regional Environment Centre to the Forestry Centre, the Forestry Centre must notify this immediately to the Regional Environment Centre, the landowner, and the known representative of the landowner and holder of the felling right." However, this kind of declaration is not needed for other species listed in the Annex IV of the Habitats Directive, e.g. bat species. Woodland areas with water may be important for bats, so this kind of declaration should also concern bat species.

The eutrophication of water usually favours Daubenton's bat (Kokurewicz 1995, Racey 1998*)*, but when it promotes excessive plant growth on the surface of the water, echolocation may gradually become difficult (Siemers et al. 2001b). Daubenton's bats typically foraged on water without plant growth on the surface, so the dredging of bodies of water with excessive plant growth favours the species, so this type of land use is acceptable in the foraging areas of the species.

In southern Finland bat surveys are typically carried out by performing 1–2 field studies during every summer month (June, July, and August). Bat populations in northern Finland are small, which may make it difficult to detect the species earlier in the summer (June and July), when the nights are brighter. Daubenton's bats avoid open areas before full darkness (Nyholm 1965) and search for dusky places to forage, and consequently the best time to map this species above 63º N would be in August, when the nights are darker and bats forage in more open habitats. The important areas to be mapped in the very northern parts of its distribution would be shady rivers flowing deep in canyons and valleys. In the Koutajoki catchment area, the rivers flow to the White Sea in Russia, and rivers serve as flight paths for Daubenton's bats, suggesting that the distribution of the species continues on the Russian side of the border. On both sides of the border there are vast uninhabited forest areas rich in small lakes (i.e. the transboundary twin parks of the Oulanka and Paanajärvi National Parks). Surveys should be carried out in the Paanajärvi region in north-western Russia to confirm this theory.

Artificial illumination attracts insects and northern bats forage these aggregations in spring and autumn (Rydell 1991, 1992b), while *Myotis* species and brown long-eared bats do not forage in illuminated areas (Rydell 1992b). Daubenton's bats avoided light places and therefore the artificial lighting of waterfronts and the bottoms of bridges should be avoided during summertime. In addition, protective tree stands should be maintained on the banks and the shore to offer shady foraging places for this species. Brandt's/whiskered bats forage in dark forests, and consequently the lighting of walkways passing through their foraging areas should be avoided during the summer months (June-August). If lighting is needed, the street lamps could be as short as possible and pointing downwards so as to illuminate only the walkway and not the forest. One of the most important things in the management of foraging areas for Daubenton's bats and Brandt's/whiskered bats in northern Europe is thus to keep them shady.

4.3 Hibernation requirements

The hibernacula in Finland housed fewer bats than in Estonia, suggesting that in Finland bats tend to be distributed over a large number of hibernacula. This strategy may give them better chances to survive when conditions change rapidly. Finnish bedrock conducts heat better, which means that frost penetrates deeper and faster, suggesting that underground conditions are perhaps more stable in Estonia. As Finland is situated further north than Estonia, the climate is colder and consequently the underground hibernacula may be warmer in Estonia.

As predicted, the species with the more southerly northern border of distribution, the pond bat, used warmer locations for hibernation than the other six species. The pond bat also hibernated in the conditions with the highest humidity and tended to hibernate in clusters. Hibernating in warmer temperatures raises the body temperature and consequently induces shorter bouts of hibernation (Wojciechowski et al. 2007). This means that the pond bat has more frequent periods of euthermy than do bats that hibernate in colder places. Bats hibernated in clusters at higher temperatures and in crevices at lower temperatures. The greatest benefit of clustering for hibernators is the reduced heat loss during arousals and subsequent periods of euthermy (Boyles et al. 2008), so the pond bat focuses on saving energy during the active periods of the hibernation season. Evaporative water loss is greater at higher body temperatures (Thomas and Cloutier 1992, Thomas 1995), so by hibernating in high-humidity conditions, the pond bat reduces evaporation and, consequently, its energy loss (Louw 1993).

Natterer's bat inhabits regions further north than those inhabited by the pond bat, but the northern border of its distribution runs further south than those of the remaining five species. In Finland, Natterer's bats inhabit regions below 62º N, whereas in Sweden, this species ranges up to 63º N (IUCN 2010). Contrary to our predictions, Natterer's bat hibernated in the coldest conditions, and our results indicate that this species tended to minimise its energy expenditure in all possible ways. Natterer's bats hibernated at temperatures closest to 2 ^{o}C, and all of them hibernated in crevices. Water loss as a result of evaporation is lowest at 2 ^{o}C and increases at both higher and lower ambient temperatures (Thomas and Geiser 1997). Evaporation increases energy loss (Thomas and Cloutier 1992, Thomas 1995), airflow increases evaporation rates by transporting water vapour away from the evaporating surface (Louw 1993), and water loss may trigger arousals (Thomas and Geiser 1997). All the Natterer's bats hibernated in crevices, which shelter bats from airflow, which in turn reduces evaporation. Natterer's bats hibernated in the driest locations, yet tended to minimise evaporation. Unlike pond bats, Natterer's bats focused on saving energy during periods of hibernation. Natterer's bats typically hibernated solitarily. Longer bouts of hibernation lead to fewer active periods during hibernation. Thus Natterer's bats do not require clustering, which saves energy during euthermic periods, as much as pond bats do.

Of the northern bat, Brandt's/whiskered bats, Daubenton's bat, and the brown long-eared bat in southern Finland and Estonia, the northern bat and the brown long-eared bat hibernated in colder and drier locations, whereas Daubenton's bat and Brandt's/whiskered bats hibernated in warmer and more humid locations. The northern bat inhabits regions further north than those inhabited by the other six species. As predicted, the northern bat typically hibernated alone on walls/ceilings (typically using no additional energy-saving methods) in cold and dry places, confirming that it is a hardy species well adapted to the harsh conditions of the north. The fact that it hibernates in cold places further suggests that it tends to save energy (long hibernation bouts), rather than to minimise the cost of hibernation (short hibernation bouts).

Brandt's/whiskered bats, Daubenton's bat, and the brown long-eared bat inhabit regions further north than those inhabited by the pond bat and Natterer's bat, but further south than those inhabited by northern bats. Brandt's/whiskered bats and Daubenton's bat hibernated in warmer locations than brown long-eared bats, suggesting that they tended to minimise the cost of hibernation more than to save energy. Brandt's/whiskered bats used both additional energy-saving methods (clusters and crevices) for hibernation both in Finland and Estonia and also clustered in crevices, as did the pond bat. Brown long-eared bats tended to save energy during hibernation (cold locations, and therefore leading to long bouts of hibernation), as did Natterer's bats, by using crevices, although less than Natterer's bats did.

Daubenton's bat was found to inhabit regions north of the Arctic Circle in the summer in this study. The fact that this species used no additional energy-saving measures (clusters and crevices) to a greater extent, as Kokurewicz (2004) has shown, suggests that Daubenton's bats may tolerate harsh conditions, despite hibernating in relatively warm and humid conditions in southern Finland and in Estonia, especially in 2006.

Previous studies have compared the hibernal conditions of these species in Europe, but none of them have compared all seven of these species. Among four *Myotis* species in Holland, Natterer's bats hibernated in the coldest conditions (mean = 6.1^{o}C), Brandt's bats (mean = 7.2 ^{o}C) and Daubenton's bats (mean=7.3 ^{o}C) in more moderate conditions, and pond bats in the warmest (mean = 7.6 ^{o}C) conditions (Daan and Wichers 1968), as in this study. Masing (1982) reports that among three *Myotis* species, pond bats (mean = 5.5 °C) hibernated in the warmest locations, Daubenton's bats (mean = 5.4 °C) in more moderate conditions, and Brandt's/whiskered bats (mean = 5.1 °C) in the coldest locations in Estonia. Among Natterer's bats, Brandt's bats/whiskered bats, and brown long-eared bats in Germany, brown long-eared bats (mean = 4.0 °C) hibernated in the coldest conditions, Brandt's bats/whiskered bats (mean = 4.6 °C) in more moderate conditions, and Natterer's bats (mean = 4.9 °C) in the warmest conditions (Nagel and Nagel 1991), unlike in our study. Bogdanowicz (1983) studied the temperatures at which brown long-eared bats, Daubenton's bats, and Natterer's bats hibernated, as well as their use of crevices in Poland. The temperatures brown long-eared bats preferred ranged from 0.5 to 4.0 °C, those preferred by Daubenton's bats from 1.5 to 6.0 °C, and in the case of Natterer's bats from 2.0 to 6.5 °C. Crevice occupation was 82.1% for the brown long-eared bat, 71.4% for Daubenton's bat, and 84.9% for Natterer's bat. Bogdanowicz and Urbańczyk (1983) found that out of brown long-eared bats, Daubenton's bats, and Natterer's bats in Poland, the mean hibernation temperature was lowest among brown long-eared bats, followed by Daubenton's bats and Natterer's bats, but Natterer's bats hibernated in the widest range of temperatures. The mean hibernation humidity was lowest in the brown long-eared bat, followed by Daubenton's bat, but highest in the case of Natterer's bat. In Poland, 89% of Natterer's bats, 85% of brown long-eared bats, and 74% of Daubenton's bats hibernated totally or partly in crevices (Bogdanowicz and Urbańczyk 1983). The fact that further south Natterer's bat hibernates in warmer conditions than the other species suggests that it employs a different hibernation strategy near the northern border of its distribution. In southern regions it tends to avoid the costs of hibernation, while in northern regions it tends to focus on saving energy.

Both in Finland and Estonia, brown long-eared bats never clustered with Daubenton's bats. In Estonia, pond bats were found to cluster only with Brandt's/whiskered bats and Daubenton's bats. Bogdanowicz (1983) suggests that the formation of multispecies clusters depends on the similarity of the ecological requirements of the species. In our study, pond bats and Natterer's bats never hibernated in the same hibernaculum, which may also indicate differences in the ecological requirements of these two species. The former searched for warmer underground sites and the latter colder ones.

An interesting question to be answered is why pond bats and Natterer's bats are so much rarer in southern Finland than in Estonia. Is it because Finnish and Estonian bedrock differs? Finnish bedrock conducts heat better, which means that frost penetrates deeper and faster, suggesting that underground conditions are perhaps more stable in Estonia. According to Webb et al. (1996), the bats' susceptibility to mortality at subzero temperatures during hibernation may limit the northerly spread of some bat species, and Natterer's bats are sometimes found frozen in Estonia (Masing and Lutsar 2007). Pond bats hibernate in warm locations, which may be difficult to find in Finland, especially in the middle of the hibernation season.

4.4 Seasonal variation in hibernation requirements

The results of this work make it evident that bats may use different hibernation strategies during the hibernation season. Early in the season, when they have large energy reserves, they minimise the costs of hibernation (short bouts of torpor) by hibernating in warmer locations. The optimal hibernation strategy for fat-storing bats is to minimise the ecological and physiological costs of hibernation by short bouts of torpor (Humpries et al. 2003, Boyles at al. 2007). This strategy is viable when relatively warm ambient temperatures are available and the bats have large energy reserves. Later in the hibernation season, bats have smaller energy reserves and are forced to minimise their energy expenditure (deeper and longer bouts of torpor) by hibernating in colder locations. This strategy is viable when relatively cold ambient temperatures are available. Several findings of this thesis support this hypothesis.

In this study, all the species hibernated in warmer locations at the beginning of the season, and colder locations in mid-season and at the end of the season, which corroborates the findings of Ransome (1968) and Kokurewicz (2004). Relatively warm ambient temperatures cause shorter bouts of torpor (optimal hibernation strategy) and cold ambient temperatures make the bouts of torpor deeper and longer (energy-saving strategy; Boyles et al. 2007).

The hibernacula were at their coldest in the middle of the hibernation season similar to the findings of Furmankiewicz and Furmankiewicz (2002) and the review in Webb et al. (1996) and became warmer towards the spring, but no species hibernated in warmer areas at the end of the season compared to the middle of the season. On the contrary, Brandt's/whiskered bats hibernated in colder locations at the end of the hibernation season than in the middle of the season, while the northern bat, Daubenton's bat, and the brown long-eared bat hibernated at similar temperatures both in the middle and at the end of the season. These results suggest that all five of these species actively selected colder temperatures (energy-saving strategy) at the end of the season. In Poland, Daubenton's bats used increasingly colder temperatures for hibernation towards spring (Kokurwicz 2004), whereas in Britain the greater horseshoe bat (*Rhinolophus ferrum-equinum;* Schreber, 1774)) used the coldest temperatures in mid-season (February; Ransome 1968). In this study, the availability of temperatures was measured at the height of two metres. Warm air rises, which means that measurements should also have been taken from the ceilings every 5 m in cases where the ceilings were higher than two metres in order to have a proper picture of the availability of temperatures.

Although the hibernacula were at their warmest at the beginning of the season and coldest in the mid-season, the range of temperatures available meant that bats could choose colder or warmer temperatures throughout the season. The extremes and range of temperatures available in the hibernacula were similar during the different portions of the season (beginning -5–10 ºC; middle -4–10 ºC; end -5–13 ºC).

This study further indicates that bats may have compensatory strategies for successful hibernation. Evaporation increases energy loss, and evaporative water loss is less at low values of body temperatures than at high ones (Thomas and Cloutier 1992, Thomas 1995). At the beginning of the season bats used the highest humidity, which, in turn, depresses evaporation, and consequently the loss of energy. Water loss may also trigger arousals (Thomas 1995), which in turn increases energy expenditure, because the bats must raise their body temperature to euthermic levels (Thomas et al. 1990). At the end of the season Brandt's/whiskered bats and Daubenton's bat used the lowest humidity, but hibernated increasingly in crevices and clusters, which in turn reduces water loss and consequently the loss of energy.

Our study verifies previous findings, which suggest that some bat species prefer thermally stable areas, while others hibernate in more variable areas (Brack 2007). This study suggests that Brandt's/whiskered bats prefer locations with stable temperatures and humidity, and shift to hibernate increasingly in these stable locations (chambers, crevices, clusters, and ceilings) towards spring. Thus it also selected warmer sites with high humidity. Temperatures and humidity in chambers are more stable than in corridors, and 52–76% of Brandt's/whiskered bats hibernated in chambers throughout the season.

Crevices shelter bats from airflow, and 79–92% of Brandt's/whiskered bats hibernated in crevices throughout the season. The greatest benefit for clustering is during arousals and subsequent periods of euthermy (Boyles et al. 2008), and 53–74% of Brandt's/whiskered bats hibernated in clusters throughout the season. Clustering increased towards spring, suggesting that bats awaken increasingly towards spring.

The ceiling area in chambers had very stable conditions, because the chambers had only one entrance (a 1.5-m-high doorway from the corridor). Brandt's/whiskered bats were especially abundant in hibernacula that had stairs leading down to a chamber, i.e. they preferred to hibernate in deeper parts of the hibernacula, where conditions were more stable. In this study, the hibernation season of Brandt's/whiskered bats was the longest one, and in stable areas the conditions are more predictable, which may help the species to survive during its long season of hibernation. The remaining three species did not move to locations with stable conditions throughout the season to such an extent as in the case of Brandt's/whiskered bats. Northern bats and Daubenton's bats joined together in clusters towards spring, suggesting that they awaken more often (saving energy through joining clusters during periods of arousal) at the end of the hibernation season, probably to observe outside temperatures (Dorgelo and Punt 1969).

4.5 Hibernation requirements – implications for land use planning

The hibernacula in Finland 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. Brandt's/whiskered bats and Daubenton's bats may gather in larger numbers to hibernate when conditions are favourable and it is extremely important to save these kinds of sites through land use planning.

The conditions inside hibernacula may vary, following the fluctuations in the outside temperature. This means that during a mild winter the conditions inside the hibernacula differ from those during a severe winter, as hibernation requirements are species-specific and further depend on the size of the energy reserves of an individual. This can cause the bats to use a hibernaculum one winter and to be absent in another year. Therefore, to make sure that an underground site is not important for bats, it should be surveyed during more than one hibernation season in case it is empty during the first year's survey.

According to EUROBATS (1998), surveys on hibernating bats should be carried out in January–February. This applies to the northern bat, Brandt's/whiskered bats, Daubenton's bat, and the brown long-eared bat, because they are most abundant in the hibernacula during these months (mid-hibernation season). However, this is not the case for Natterer's bats. This study pointed out that the most appropriate time to find this species in southern Finland is at the end of October, when the bats can be found in crevices in the hibernacula, especially in the entrance areas. Natterer's bats are scarce in Finland, which makes it difficult to detect the species with bat detectors in the summertime. Most of the hibernating Natterer's bats were found in south-eastern Finland, which suggests that the species is probably more abundant there.

The pond bat was found to occur in Finland. This species is listed in Annex II of the Habitats Directive, which means that its conservation requires the designation of special areas of conservation. More specimens of pond bats can probably be found especially in south-eastern Finland, because in the St. Petersburg region in Russia this species hibernates in larger numbers (Strelkov 1970). When bat surveys are carried out near the border to Russia in southern Finland, the presence of pond bats should be studied.

Populations and population trends in bats are particularly difficult to measure. According to this study the conditions inside hibernacula, even in chambers (which have the most stable conditions), may vary according to the outside weather, which in turn affects the number of bats inside the hibernacula, since bats have species-specific hibernation requirements. As the numbers of bats in a hibernaculum may vary according to the weather outside, one should be very careful when drawing conclusions about population changes from the yearly monitoring results of hibernacula. As both the conditions in winter roosts and the hibernal requirements of bats keep on changing during the hibernation season, the number of bats in Finnish hibernacula may vary from year to year. This makes it difficult to monitor bat populations through counting them in underground sites.

Bats typically used natural stone for hibernation. Few hibernation sites have been found in Finland so far, suggesting that bats may hibernate in natural places, e.g. holes in steep rock faces. When planning a development it is therefore advisable to survey natural underground sites in rocks or cliffs or man made underground sites built using natural stone to find out if these sites are important for bats.

All the bats, especially Natterer's bats and Brandt's/whiskered bats, used crevices for hibernation. For Brandt's/whiskered bats and Natterer's bats it would be appropriate to save underground sites made of natural stone with a lot of tight crevices, because these species mostly hibernate in narrow cracks where they can have body contact with walls on all sides. For the brown long-eared bat underground sites made of natural stone with bigger holes are also important, since they were found to use large crevices where they could hang from the crevice ceiling by their hind feet without having any other contact with the substrate.

As bats commonly used crevices in natural stone for hibernation, they can also hibernate in rock scree in northern Europe, as suggested by Michaelsen and Grimstad (2008), and consequently these sites should be surveyed if possible when deciding the use of land if background information suggests that they may be present.

Bats have species-specific hibernation requirements and strategies, which may change during the hibernation season and according to the geographical region. In this study the patterns among species remain the same: northern bats and brown long-eared bats hibernated in colder and drier places, whereas Brandt's/whiskered bats and Daubenton's bat hibernated in warmer and more humid sites, both in Finland and Estonia. All this variation makes mitigation (the reduction or prevention of damage) or compensation (offsetting the damage caused by development, e.g. the creation of new roosts) difficult, although the results of this study can be used when manipulating conditions in hibernacula to make them more suitable for a species or when designing completely new artificial winter roosts. Thus avoiding damage to existing winter roosts is always the most appropriate way to take bats into account when planning a development.

REFERENCES

Addison, A. & Sprouse, P. 2007. 3D data collection for characterization of bat habitat. Proceedings of the 2007 National Cave and Karts Management Symposium: 13–16.

Ahlén, I. 1981. Identification of Scandinavian bats by their sounds (Report 6). Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Uppsala, Sweden: 1–56.

Ahlén, I. 2004. The bat fauna of Sweden. Present knowledge of distribution and status. Kunskapsläget 2004. Fauna och Flora 99: 2-11. [In Swedish].

— & Gerell, R. 1989. Distribution and status of bats in Sweden. In: Hanák, V. Horáček, I. and Gaisler, J. (eds.). European bat research 1987. Charles Univeristy Press, Prague. p. 319–325.

Ahti,T., Hämet-Ahti, L. & Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5: 169–211.

Anderson, M.E. & Racey, P.A. 1991. Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. Animal Behaviour 42: 489–493.

Arnold, W. 2007. The evolution of marmot sociality: II. Cost and benefits of joint hibernation. Behavioral Ecology and Sociobiology. 27: 239–246.

Avery, M.I. 1985. Winter activity of pipistrelle bats. Journal of Animal Ecology 54: 721–738.

Baagøe, H. J. 1987. The Scandinavian bat fauna.: adaptive wing morphology and free flight in the field. Pp. 57-74 in: Recent Advances in the Study of Bats (M. B. fenton, P. Racey, and J.M.V. Rayner, eds.). Cambidge University Press, Cambridge. 470 p.

Barataud, M. 1990. Eléments sur le comportement alimentaire des Oreillards brun et gris, *Plecotus auritus* (Linnaeus, 1758) et *Plecotus austriacus* (Fischer, 1829). Le Rhinolophe 7: 3–10.

Barnard, C. 2004. Animal Behaviour. Mechanism, development, Function and Evolution. Pearson Education Limited. Essex. 726 p.

Beck, A. 1995. Fecal analyses of European bat species. Myotis 32–33: 109–119.

Bogdanowicz, W. 1983. Community structure and interspecific interactions in bats hibernating in Poznań. Acta Theriologica 28: 357–370.

— & Urbańczyk, Z., 1983. Some ecological aspects of bats hibernating in city of Poznań. Acta Theriologica 28: 371–385.

Boyles, J.G., Dunbar, M.B., Storm, J.J. & Brack, V. Jr. 2007. Energy availability influences microclimate selection of hibernating bats. Journal of Experimental Biology 210: 4345–4350.

— , Storm, J.J. & Brack, V. Jr. 2008. Thermal benefits of clustering during hibernation: a field test of competing hypotheses on *Myotis sodalis*. Fuctional Ecology 22: 632–636.

Brack, V. Jr. 2007. Temperatures and locations used by hibernating bats, Including *Myotis sodalis* (Indiana Bat), in Limestone Mine: Implications for Conservations and Management. Environmental Management 40: 739–746.

Bradbury, J. & Nottebohm, F. 1969. The use of vision by the little brown bat, *Myotis lucifugus*, under controlled conditions. Animal Behaviour 17: 480-485.

Choi, I.-H., Cho, Y., Oh, Y.K., Jung, N.-P. & Shin, H.-C. 1998. Behavior and muscle performance in heterothermic bats. Physiological and Biochemical Zoology 71: 257–266.

Clawson, R. L., Laval, R. K., Laval, M. L. & Caire, W. 1980. Clustering behavior of hibernating *Myotis sodalis* in Missouri. Journal of Mammalogy 61: 245–253.

Daan, S. 1973. Activity during natural hibernation in three species of vespertilionid bats. Netherlands Journal of Zoology 23: 1–71.

— , Barnes, B.M. & Strijkstra, A.M. 1991. Warming up for sleep – ground squirrels sleep during arousals from hibernation. Neuroscience Letters 128: 265–268.

— & H. J. Wichers 1968. Habitat selection of bats hibernating in a limestone cave. Z. Säugetierk. 33: 262–287.

de Jong, J. 1995. Habitat use and species richness of bats in a patchy landscape. Acta Theriologica 40: 237–248.

Dorgelo, J. & Punt, A. 1969. Abundance and "internal migration" of hibernating bats in an artificial limestone cave ("Sibbergroeve"). Lynx 10: 101–125.

Drebs, A., Nordlund, A., Karlsson, P., Helminen, J. & Rissanen, P. 2002. Tilastoja Suomen ilmastosta 1971–2000 - Climatological statistics of Finland 1971–2000. Finnish Meteorological Institute, Helsinki: 1–100.

Eesti Meteoroloogia ja Hüdroloogia Instituut 2010. Available at: http://www.emhi.ee. [Cited 31 November 2010].

Eklöf, J. & Jones, G. 2002. Use of vision in prey detection by brown long-eared bats, *Plecotus auritus*. Animal Behaviour 66: 949–953.

Eklöf, J., Svensson, A.M. & Rydell, J. 2002. Northern bats (Eptesicus nilssonii) use vision but not flutter-detection when searching for prey in clutter. Oikos 99: 347-351.

Ellins, S.R. & Masterson, F.A. 1974. Brightness discrimination thresholds in the bat, Eptesicus fuscus. Brain, Behavious and Evolution 9: 248-263.

Estonica. 2009. [Internet site]. Climate. Estonica. Encyclopedia about Estonia. Available at: http://www.estonica.org. [Cited 31 November 2010].

EUROBATS. 1998. Consistent Monitoring Methodologies. Doc. EUROBATS.MOP2.5. Available at: http://www.eurobats.org. [Cited 31 November 2010].

EUROBATS. 2004. Protecting and managing underground sites for bats, Doc.EUROBATS.AC9.15. Available at: http://www.eurobats.org. [Cited 31 November 2010].

EUROBATS. 2009. Agreement on the conservation of populations of European bats. Update to the National implementation report of Finland. Inf.EUROBATS.AC14.11. Available at: http://www.eurobats.org. [Cited 31 November 2010].

Fenton, M.B. 1990. The foraging behaviour and ecology of animals eating bats. Canadian Journal of Zoology 68: 411–422.

— 1995a. Natural history and biosonar signals. In: Popper, A.N. & Fay, R.R. (eds). Hearing by Bats. Springer-Verlag, New York. p. 37–86.

— 1995b. Constraint and flexibility – bats as predators, bats as prey. In: Racey, P.A & Swift, S.M. (eds). Ecology, Evolution and Behaviour of Bats. Proceedings of Symposia Zoological Society of London 67: 277–289.

Finnish Environment Institute 2010. Species listed in Annexes II, Iv and V of the EU's Habitat Directive. Available at: http://www.ymparisto.fi/. [Cited 31 November 2010].

Fluckiger, P.F. & Beck, A. 1995. Observations on the habitat use for hunting by *Plecotus austriacus* (Fischer, 1829). Myotis 32–33: 121–122.

Frerichs, K.U., Smith, C.B., Brenner M., DeGargia, D.J., Krause, G.S., Marrone, L., Dever, T.E. & Hallenbeck, J.M. 1998. Supression of protein synthesis in brain during hibernation involves inhibition of protein initiation and elongation. Proceedings of the National Academy of Sciences of the United States of America 95: 14511–14516.

Furmankiewicz, J. & Furmankiewicz, M. 2002. Bats hibernating in the natural caves in the Polish part of the Sudetes. Przyroda sudetów zachodnich suplement 2: 15–38..

Gaisler, J., Zukal, J., Nesvadboda, J. Chytil, J. & Obuch, J. 1996. Species diversity and relative abundance of small mammals (Insectivora, Chiroptera, Rodentia) in the Palava biosphere reserve of UNESCO. Acta Societas Zoologicae Bohemicae 60: 13–23.

Griffin, D. R. 1958. Listening in the dark: the acoustic orientation of bats and men. Yale University Press, New Haven. New Haven, CT. 413 p.

Haupt, M., Menzler, S. & Schmidt, S.D. 2006. Flexibility of habitat use in *Eptesicus nilssonii*: Does the species profit from anthropogenically altered habitats? Journal of Mammalogy 87: 351–361.

Hill, R.A., Hinsley, S.A. & Bellamy P.E. 2007. Integrating multiple datasets for the remote quantifications of woodland bird habitat quality. International Archives of

Photogrammetry, Remote Sensing and Spatial Information Sciences 36 (8/W2): 248–253.
Hitchcock, H.B. 1949. Hibernation of bats in southeastern Ontario and adjacent Quebec. Canadian Field-Naturalist 63: 47–59.
Hock, R.J. 1951. The metabolic rates and body temperature of bats. Biological Bulletin 101: 289–299.
Humpries, M.M., Thomas, D.W. & Kramer, D. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. Physiological and Biochemical Zoology 76: 165–179.
Iso-Iivari, L. 1988. Vertebrates of Inari Lapland. Kevo Notes 1(3rd ed.): 1–12.
IUCN 2010. IUCN Red List of Threatened Species. Version 2010. 1. Available at: www.iucnredlist.org. [Cited 31 November 2010].
Jones, G. & Rayner, J.M.V. 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bat *Myotis daubentonii* (Chiroptera: Vespertilonidae). Journal of Zoology (London) 215: 113–125.
Kalko, E.K.V & Schnitzler, H.U. 1989. The echolocation and hunting behaviour of Daubenton's bat, *Myotis daubentonii*. Behavioral Ecology and Sociobiology 24: 225–238.
Kokurewicz, T. 1995. Increased population of Daubenton's bat *Myotis daubentonii* (Kuhl, 1819). (Chiroptera: Vespertilionidae) in Poland. Myotis 32–33: 155–161.
— 2004. Sex and age related habitat selection and mass dynamics of Daubenton's bats *Myotis daubentonii* (Kuhl, 1817) hibernating in natural conditions. Acta Chiropterologica 6: 121–144.
Kunz, T.H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology 55: 639–711.
Lausen, C.L. & Barclay, R.M.R. 2006. Winter bat activity in the Canadian prairies. Canadian Journal of Zoology 84: 1079–1086.
Limpens, H. & Kapteyn, K. 1991. Bats, their behavious and linear landscape elements. Myotis 29: 39-48.
Louw, G.N. 1993. Physiological Animal Ecology, Longman Scientific and Technical, Essex. 288 p.
Luis, A.D. & Hudson, O.J. 2006. Hibernation patterns in mammals: a role for bacterial growth? Functional Ecology 20: 471–477.
Lyman, C.P., Willis, J.S., Malan, A. & Wang, L.C.H. 1982. Hibernation and Torpor in Mammals and Birds. Academic Press, New York. 328 p.
Magurran, A. 2007. Measuring Biological Diversity. Blackwell Publishing, Oxford. p. 114–116.
Masing, M. 1982. On the air temperature at hibernation sites of bats. Eesti ulukid. Eesti Terioloogia Selts, Tartu. p. 67–74. [In Estonian]
— 1984. Bats. Pääsuke, Tallinn. 112 p. [In Estonian].
— & Lutsar, L. 2007. Hibernation temperatures in seven species of sedentary bats (Chiroptera) in northeastern Europe. Acta Zoologica Lituanica 17: 47–55.
McNab, B.K. 1974. The behaviour of temperate cave bats in a subtropical environment. Ecology 55: 943–958.
Michaelsen, T.C. & Grimstad, K.J. 2008. Rock scree – a new habitat for bats. Nyctalus 13: 122–126.
Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger F., Stubbe M., Thissen, J.B.M., Vohralík V. & Zima, J. 1999. The Atlas of European Mammals. T. & A.D. Poyser, London. p. 110–111, 140–141.

—, A.J., Bihari, Z. Masing, M. & Rodrigues, L. 2007. Protecting and managing underground sites for bats. Eurobats Publication Series 2: 1–38.

Munro, D., Thomas, D.W. & Humpries, M.M. 2005. Torpor patterns of hibernating eastern chipmunks *Tamius striatus* vary in response to the size and fatty acid composition of food hoards. Journal of Animal Ecology 74: 692–700.

Nagel, A. & Nagel, R. 1991. How do bats choose optimal temperatures for hibernation? Comparative Biochemistry and Physiology Part A: Physiology 99: 323–326.

Neuweiler, G, 1989. Foraging ecology of and audition in echolocating bats. Trends in Ecology and Evolution 4: 160-166.

Nyholm, E. S. 1965. Ecology of *Myotis mystacinus* and *M. daubentonii* (Chiroptera). Annales Zoologici Fennici 2: 77–123. [In German].

Obrist, M. K., Boesch & Flückiger, P. F. 2004. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. Mammalia 68: 307–322.

Pettersson Elektronik Ab. 2004. Sound analysis programme. Pettersson Elektronik Ab, Uppsala.

Racey, P.A. 1998. The importance of the riparian environment as a habitat for British bats. In: Dunstone, N. & Norman, M.L (eds). Behaviour and ecology of riparian mammals.. Symposia of the Zoological Society of London 71: 69–91.

Ransome, R. 1968. The distribution of the greater horseshoe bat, *Rhinolophus ferrumequinum*, during hibernation, in relation to environmental factors. Journal of Zoology (London) 154: 77–112.

Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. 2001. The Red List of Finnish Species. Ministry of the Environment & Finnish Environment Institute, Helsinki. 432 p.

Rydell, J. 1986. Foraging and diet of the northern bat *Eptesicus nilssoni* in Sweden. Holarctic Ecology 9: 272–276.

— 1989. Food habits of northern (*Eptesicus nilssoni*) and brown long-eared (*Plecotus auritus*) bats in Sweden. Holarctic Ecology 12: 16–20.

— 1991. Seasonal use of illuminated areas by foraging northern bats Eptesicus nilssonii. Holarctic Ecology 14: 203–207.

— 1992a. Ocurrence of bats in northernmost Sweden (65°C) and their feeding ecology in summer. Journal of Zoology (London) 227: 517–529.

— 1992b. Exploitation of insects around streetlamps by bats in Sweden. Functional Ecology 6: 744–750.

— , Entwistle, A. & Racey, P.A. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76: 246 –252.

— , Miller, L.A. & Jensen, M.E. 1999. Echolocation constraints of Daubenton's bat foraging over water. Functional Ecology 13: 247–255.

Rydell, J. & Speakman, J.R. 1995. Evolution of nocturnality in bats: potential competitors and predators during their early history. Biological Journal of the Linnean Society 54: 183–191.

Schnitzler, H-U. & Kalko, E.K.V. 1998. How echolocating bats search and find food. In: Kunz, T.H. & Racey, P.A. (eds). Bat Biology and Conservation. Smithsonian Institution Press, Washington DC. p 183–196.

— & Kalko, E.K.V. 2001. Echolocation by insecteating bats. Bioscience 51: 557–569.

— , Moss, C.F. & Denzinger, A. 2003. From spatial orientation to food acquisition in echolocating bats. TRENDS in Ecology and Evolution 18: 366–394.

Shiel, C.B., McAney, C.M. & Fairley, J.S. 1991. Analysis of the diet of Natterer's bat *Myotis nattereri* and the common long-eared bat *Plecotus auritus* in the west of Ireland. Journal of Zoology (London) 223: 299–305.
Siemers, B. M. & Schnitzler, H.-U. 2000. Natterer's bat (*Myotis nattereri* Kuhl, 1818) hawks for prey close to vegetation using echolocation signals of very broad bandwidth. Behavioral Ecology and Sociobiology 47: 400–412.
— , Dietz, C., Nill, D. & Schnitzler, H.-U. 2001a. *Myotis daubentonii* is able to catch small fish. Acta Chiropterologica 3: 71-75.
— , Stilz, P. & Schnitzler, H.-U. 2001b. The acoustic advantage of hunting at low heights above water: behavioural experiments on the European 'trawling' bats *Myotis capaccinii, M. dasycneme* and *M. daubentonii*. The Journal of Experimental Biology 204: 3843–3854.
Siivonen, L. & S. Sulkava 1999. Mammals of the North. Otava, Helsinki. 224 p. [In Finnish].
Siivonen, Y. 2001. Bat survey in the city of Järvenpää 2001–2002, vaihe I:n raportti joulukuu 2001. City of Järvenpää. 6 p. [In Finnish].
— 2004. Bat species and areas frequently used by bats in the city of Helsinki in the year of 2003. Helsingin kaupungin ympäristökeskuksen julkaisuja 3/2004. City of Helsinki. 36 p. [In Finnish].
Simmons, J.A. & Stein, R.A. 1980. Acoustic Imaging in bat sonar: echolocation signals and the evolution of echolocation. J. Comp. Physiol. A. 135: 61-84.
Söderman, T. 2003. Biodiversity impact assessment in regional planning, environmental impact assessment and Natura 2000 assessment. Ympäristöopas 109. Suomen ympäristökeskus, Helsinki. 196 p. [In Finnish].
Speakman, J.R. 1991. Why do insectivorus bats in Britain not fly in daylight more frequently? Funct. Ecol. 5: 518524.
— 1995. Chiropteran nocturnality. In: Racey, P.A. and Swift, S.M. (eds). Ecology, evolution and behaviour of bats. Symp. Zool. Soc. Lond. No. 67. Clarendon Press, Oxfored, pp. 187–201.
Speakman, J.R., Rydell, J., Webb, P.I., Hayes, J.P. & Hays, G.C, Hulbert I.A.R. &. McDevitt R.M. 2000: Activity patterns of insectivorous bats and birds in northern Scandinavia (69°N), during continuous midsummer daylight. Oikos 88: 75–86.
Statistics Finland 2005. Land use 1960-1999. Statistical yearbook of Finland 2004. Tilastokeskus, Helsinki. p. 1–54.
Strelkov, P.P. 1970. Chiroptera. In: Novikov, G. A., Airapetjantz, A. E., Pukinsky, Ju., Strelkov, P. P. & Timofeeva, E. K. (eds.). Mammals of Leningrad. Leningrad State University Press, Leningrad. p. 63–84. [In Russian].
Swift, S.M. 1998. Long-Eared Bats. T. & A.D. Poyser, London. 182 p.
— & Racey, P.A. 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. Journal of Zoology (London) 200: 249–259.
— & Racey, P.A. 2002. Gleaning as a foraging strategy in Natterer's bat *Myotis nattereri*. Behavioral Ecology and Sociobiology 52: 408–416.
The Almanac Office at University of Helsinki. 2010. Finnish calendar 2010. Available at: http://almanakka.helsinki.fi. [Cited 31 October 2010].
Thomas, D.W. 1995. The physiological ecology of hibernation in vespertilionid bats. Symposia of the Zoological Society of London 67: 233–244.
— & Cloutier, D. 1992. Evaporative water by hibernating little brown bats, *Myotis lucifugus*. Physiological Zoology 65: 443–456.
— , Dorais, M. & Bergeron, J. 1990. Winter energy budgets and costs of arousals for hibernating little brown bats, *Myotis lucifugus*. Journal of Mammalogy 71: 475–479.

— & Geiser, F. 1997. Periodic arousals in hibernating mammals: is evaporative water loss involved? Functional Ecology 11: 585–591.

Trachsel, L., Edgar, D.M. & Heller H.C. 1991. Are Ground-squirrels sleep-deprived during hibernation. American Journal of Physiology 260: 1123–1129.

Twente, J.W. 1955. Some aspects of habitat selection and other behaviour of cavern dwelling bats. Ecology 36: 706–732.

van Breukelen, F. & Martin, S.L. 2002. Reversible depression of transcription during hibernation. Journal of Comparative Physiology B 172: 355–361.

Webb, P. I., Speakman, J.R. & Racey, P.A. 1996. How hot is a hibernaculum? A review of the temperatures at which bats hibernate. Canadian Journal of Zoology 74: 761–765.

Wojciechowski, M.S., Jefimow, M. & Tęgowska, E. 2007. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). Comparative Biochemistry Physiology 147A: 828–840.