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Anni Rautio

On the northern edge – ecology of urban hedgehogs in eastern Finland

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ABSTRACT

The European (Western) hedgehog (*Erinaceus europaeus*) is a hibernating insectivore with a fairly wide geographical distribution, occurring under a great variety of climatic conditions. Its populations in Finland result from intentional introductions, and the long, harsh winters impose limits on its survival in the north. Despite its wide distribution, most research on hedgehogs has been conducted in more southerly areas and its ecology in Northern Europe is poorly known. The main aim of this thesis was to study the ecology of the hedgehog living in an urban environment at the northern limit of its distribution range. Its behavioural ecology and annual activity patterns were studied by radio tracked hedgehogs, and mortality factors, diseases, parasites, diet and environmental pollutants were studied from hedgehog carcasses.

Hedgehogs had large home ranges at northern latitudes and the number of nests was greater than further south. The average size of a male's home range during the active period was 98 ha and that of a female's 55 ha. Both the size of the home range and the number of nests, changed during the active period. Nests are especially important for hedgehogs in the harsh northern environment. Nests were typically in residential areas in summer.

The hedgehogs had a clear transition period in late summer before settling down in their hibernation nest. During this period they moved away from the residential areas to the forests, where they constructed several pre-hibernation nests. The average length of the hibernation period was eight months. The males (858 g) were heavier than the females (757 g), and after the short mating season they gained weight during the rest of the active period. Females first raised their offspring and then started to build up fat reserves.

Hedgehogs were the most frequent small mammals killed on the roads, with no difference between the sexes in road-kill frequencies. Females died on the roads most often in late summer, when they started to enlarge their home range after weaning their offspring. Newly independent juveniles were most often traffic victims in the autumn. Habitat type and the speed limits did not appear to affect the road death frequencies. Of the natural mortality factors, starvation among the juveniles and purulent, gangrenous inflammation in the paws of adult males were typical. Lungworms (*Crenosoma striatum*) were the most common endoparasites. The natural diet consisted of invertebrates such as beetles and earthworms, but vertebrates were also consumed. Food provided by humans played a major part in the diet. Hygiene at feeding sites is very important, since over half of the hedgehogs examined had a *Salmonella* infection.

Concentrations of metals, arsenic and selenium were generally low, but a clear age-related accumulation of heavy metals such as cadmium was found even though the area concerned was comparatively unpolluted. Hedgehogs are at risk from environmental pollution due to accumulation of metals with age, and can be used as bioindicators of metal pollution.

In Northern Europe, hedgehogs have large home ranges during the short and intensive active season in which species reproduce and gain energy for the very long hibernation period. Hedgehogs have integrated well in urban and sub-urban areas in terms of their behavioural ecology and they are able to take advantage of man-made environments for both food and nest sites. However, intensive interaction with humans also includes negative effects on hedgehogs including e.g. traffic mortality and zoonoses.

Universal Decimal Classification: 574.2, 591.5, 599.365

CAB Thesaurus: Erinaceus europaeus; animal ecology; animal behaviour; nests; habitats; movement; telemetry; mortality; parasites; Salmonella; diet; heavy metals; hibernation; Finland

Yleinen suomalainen asiasanasto: siilit; eläinekologia; käyttäytyminen; pesät; elinympäristö; habitaatti; elinpiirit; liikkuminen; seuranta; kuolemansyyt; loiset; Salmonella-bakteerit; ravinto; raskasmetallit; kertyminen; horros; Suomi

Preface

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A considerable part of this thesis was spent in the night of Joensuu with hedgehogs, mosquitos and local people interested in hedgehogs. Thanks are due to the town of Joensuu and many local people for their cooperation. Nothing would have happened in the field without several people. I am grateful to Ari Kirjavainen, Pia Rännänen, Marja Haatanen and Miina Auttila for their tireless work in radio tracking hedgehogs and to Harri Kirjavainen and Mirva Ikonen who did huge work searching and collecting hedgehog carcasses. I wish to thank radio amateur Heikki Jeronen for constructing and repairing the radio tracking equipment. The Co-authors Marja Isomursu and Varpu Hirvelä-Koski are also gratefully acknowledged. Thanks are also due to Jani Sormunen and Anu Hakala for identifying ticks.

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This thesis is dedicated to my parents, Hely and Pauli who have always supported me whatever I have done in my life. I wish to thank my dear sister Marja and her family for their support and my brother Juha-Pekka and his wife Leila for nice conversations and help with the graphics. My final thanks go to Juho, for his love, patience and support and our son Roope, who reminds me everyday what is most important in life.

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman numerals I-IV.

I Rautio A, Valtonen A, Kunnasranta M. The effects of sex and season on home range in European hedgehogs at the northern edge of the species range. *Annales Zoologici Fennici 50: 107-123, 2013.*

II Rautio A, Valtonen A, Auttila M, Kunnasranta M. Nesting patterns of European hedgehogs (*Erinaceus europaeus*) under northern conditions. *Acta Theriologica 59: 173–181, 2014.*

III Rautio A, Isomursu M, Valtonen A, Hirvelä-Koski V, Kunnasranta M. Mortality, diseases and diet of hedgehogs (*Erinaceus europaeus*) under human influence in Finland. Submitted manuscript.

IV Rautio A, Kunnasranta M, Valtonen A, Ikonen M, Hyvärinen H, Holopainen IJ, Kukkonen JVK. Sex, age, and tissue specific accumulation of eight metals, Arsenic, and Selenium in the European hedgehog (*Erinaceus europaeus*). *Archives of Environmental Contamination and Toxicology 59: 642–651, 2010.*

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AUTHOR'S CONTRIBUTION

The author of this thesis contributed to the planning of all the papers (I-IV) and played a major role in collecting the data for papers I-II and a minor role for papers III-IV. She assisted in the metal analyses for paper IV. She was responsible for analysing the data for all papers. She wrote the manuscripts, with significant editorial input from all the co-authors (I-IV).

Contents

1 Introduction

In northern latitudes, after short growing season comes the long and cold winter and this is the most stressful time of year for most forms of life. There are different strategies to surviving difficult conditions such as migration, movement through winter and dormancy. The ecology of hibernating species is particularly affected by northern latitude because active season for reproduction and energy storing is extremely short. In Northern Europe, for example in the southern boreal zone, the growing season is only 130-140 days and in arctic under 100 days (Karlsen et al., 2006). Increasing latitude is also associated to lower net primary productivity (Huston & Wolverton, 2009). Low food productivity means that an animal have to meet its energy requirement in a larger home range than an animal living in area of high food productivity (Dahle & Swenson 2003; Kauhala et al., 2005).

Urban and sub-urban settlements are expected to house increasing numbers of people and at higher densities (World Urbanization Prospects, 2008) and the expansion of these areas is typically expected to be detrimental to global biodiversity (Harrison & Davies, 2002; DeStefano & DeGraaf, 2003). Mammalian species living in these areas are dependent on their ability to survive and reproduce in extensively modified landscapes, and are also influenced by patterns of human tolerance and conflict (Baker & Harris, 2007).

Urban and sub-urban patches of semi-natural or natural habitats and substantial areas of private residential gardens can provide habitats for a range of mammalian species (Baker & Harris, 2007), and animals can also take advantage of human waste and supplementary feeding (Prange et al., 2004; Reeve & Morris, 1985). A high concentration of artificial food sources has been observed to contribute to reduced home-range sizes and increased population densities (Prange et al., 2004). On the other hand, the constant fragmentation of green spaces and decline in garden structures can have a negative effect on mammalian species (Baker & Harris, 2007). Also, urban and sub-urban areas are often characterized by a high degree of pollution, so that insectivores, for example, are easily exposed to environmental toxins (Pankakoski et al., 1994; Komarnicki, 2000; D'Havé et al., 2006).

The prevalence of diseases and parasites is greater in urban wildlife than in rural habitats, and these can be transmitted easily to humans and to companion animals in dense urban mammal populations (Handeland et al., 2002; Egli, 2004; Ditckoff et al., 2006). Similarly, mortality due to traffic is suggested to be high in densely populated areas because of very dense road networks and high levels of traffic flow (Forman & Alexander, 1998; Holsbeek et al., 1999). With increasing numbers of wildlife species and wildlife-human conflicts in urban areas, it is becoming essential to develop a better understanding of the ecology of urban mammals.

1.1 THE EUROPEAN HEDGEHOG

The European (Western) hedgehog (*Erinaceus europaeus*) is a hibernating, solitary, nocturnal small mammal, occurring in the British Isles and the Iberian peninsula, westwards through much of western to central Europe; and from southern Fennoscandia, and the northern Baltic to north-west Russia (Amori et al., 2013). It is nowadays protected in many countries and is generally accepted by humans, although in New Zealand it is an alien species and is regarded as a pest (Jones et al., 2005; Recio et al., 2013). In Finland, hedgehogs are living at the northernmost limit of their distribution range (Kristiansson, 1981), having been actively introduced here by man over 100 years ago on the assumption that they kill snakes and rats (Kristoffersson et al., 1966; Kristiansson, 1981).

Its specialized back muscles and sharp spines are features that enable the hedgehog to roll up and defend itself highly effectively against predators (Reeve, 1994). Olfaction and hearing are its dominant senses, but vision and its long whiskers are also important. Probably because of the spines, it has only a few natural predators, such as the badger (*Meles meles*) and the eagle owl (*Bubo bubo*) (Marchesi et al., 2002; Hof, 2009). Its natural habitats include deciduous woodland, scrub and moist grassland (Corbet, 1988), but it is well adapted to man-made habitats and is a frequent visitor to farms, horticultural areas, parks and domestic gardens, even in densely populated suburbs. The hedgehog uses most of its active time during the night for foraging (Reeve, 1994; Riber, 2006), and the network of nests that it constructs across its home range provides both concealment and protection from the weather (Reeve, 1994).

The hibernation period is a time of lowered metabolism, the hedgehog's heartbeat, for example, decreases from 200-280 to 2-12 beats per minute (Eklund et al., 1972; Kristoffersson & Soivio, 1964). This period varies in length according to climate, individual condition and sex, being longer under harsh climatic conditions than in milder areas, where some individuals may remain active almost all the year round (Parkes, 1975; Jensen, 2004; Haigh et al., 2012).

Urban districts with abundant green areas may have a higher hedgehog population density than any natural habitat would ever have, whereas urban centres with little vegetation have low densities (Huijser, 2000; Hubert et al., 2011). In general, urban environments are highly heterogeneous and tend to be warmer than the surrounding areas (Wilby, 2003). In Finland the species is considered to live mainly in man-made habitats. On the other hand, hedgehogs are under considerable pressure in urban areas from anthropogenic factors such as pollution, traffic and habitat fragmentation (Huijser & Bergers, 2000; D'Have et al., 2006; Dowding, 2007).

Hedgehog numbers have decreased considerably in more southerly areas, a trend that has been mainly correlated with an increase in badger abundance, and the loss and fragmentation of suitable habitats (Hof, 2009). The ecology of the species in Northern Europe is poorly known (Kristiansson, 1984), and there is a great need for information on the ecology and behaviour of these animals in order to ensure their protection.

1.2 OBJECTIVES OF THIS STUDY

The aim of this thesis was to study the behavioural ecology of hedgehogs under northern conditions and interactions between humans and hedgehogs in an urban area. The specific objectives were:

1. Home-range sizes and overlaps, movements, and nest-use behaviour of hedgehogs were studied to determine species seasonal habitat use and activity patterns (I, II).
2. The diet, occurrence of diseases, parasites and bacteria, and natural and human related mortality factors of hedgehogs were investigated with emphasis on interaction with humans in urban area (III).
3. Concentrations of environmental pollutants in hedgehogs were studied to evaluate species exposure to environmental pollution (IV).

2 Materials and Methods

2.1 STUDY AREA

The research was conducted in Joensuu (63°N, 29°E), a medium-sized town in Eastern Finland with a population of 73,000 (Fig. 1A). The area of about 7 km^2 used for radio tracking (Fig. 1A) consisted mainly built-up areas (77%) and forest and semi-natural areas (23%). During the study period (2004-2006) the ground was covered with snow for about five months annually from the end of November to the end of April. The route for the traffic mortality survey included a variety of speed limit zones (30-100 km/h) and surrounding habitat types: residential areas, other built-up areas and forest (Fig. 1A).

2.2 VHF AND BODY WEIGHT MONITORING

The hedgehogs for the radio telemetry study were captured by hand or in wooden mink traps and anaesthetized (I, II). They were weighed, sexed, marked with uniquely numbered plastic ear tags and checked for injuries. The transmitters (Biotrack, model TW-3, UK) were glued directly to a mid-dorsal patch of clipped spines. The tagged hedgehogs (13 males, 12 females) were all defined as sexually mature (individuals that had hibernated at least once), and they carried the transmitters for periods ranging from four days to > 1 year, with eleven individuals hibernating with their transmitters. During the active period, tracking was initiated before the hedgehogs emerged in the evening and terminated after the last individuals had retreated into their day nests the following morning, locations being checked about every two hours. The animals were typically tracked from a distance of ≤ 30 m and were often observed visually.

The tracked hedgehogs were weighed approximately every two weeks. In addition, weight data for ear-tagged hedgehogs without radio transmitters (82 males, 77 females) were also collected in the same area (I).

2.3 HOME RANGE ESTIMATION

Home-range sizes during the active period (April–September for males and May–October for females) and separate home-range sizes for the three seasons (mating season: 1 May–15 June, post-mating season: 16 June–31 July and pre-hibernation season: 1 August–15 September) were calculated from the radio telemetry data (I). A 95% fixed kernel (K95) was considered to represent the total home range and a 50% kernel (K50) the core area (Fig. 1B). Minimum convex polygons (100%) (MCP100) were used to obtain a better comparison with previous hedgehog home-range studies.

The spatial organization of the hedgehogs' home ranges was studied by overlap analysis, considering the percentage overlap between each pair of home ranges (K95, K50 and MCP100) and the overlap of home ranges between the seasons for each individual (I). Home-range centre shift data for each individual were also studied.

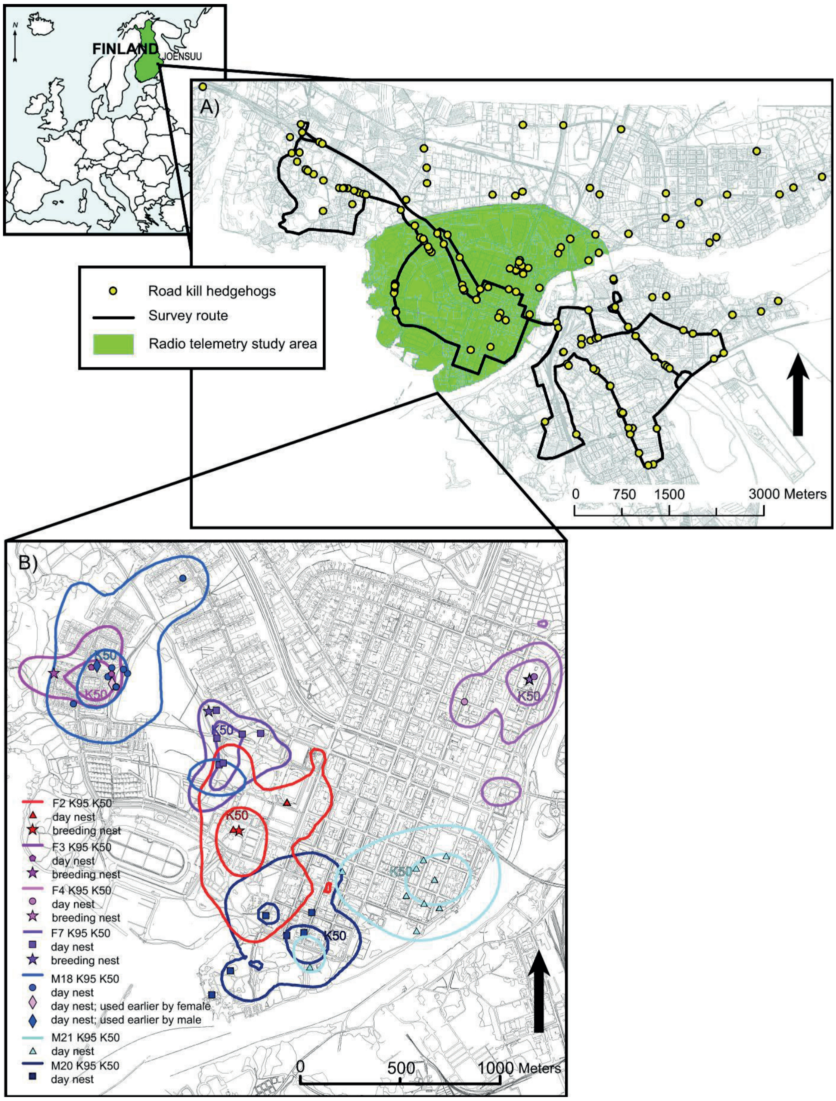

Figure 1 *A) Road kill hedgehogs collected from survey routes and other locations in town of Joensuu and radio telemetry study area. B) Examples of the total home ranges (K95), core areas (K50) of hedgehogs and different types of nests used during the post-mating season.*

2.4 NEST TYPES AND NESTING BEHAVIOUR

The nest sites of the radio-tracked individuals were identified between dawn and dusk during the active period (II; Fig. 1B), and the winter-time locations of the hibernating hedgehogs were checked at monthly intervals. Nest types were divided into four functional categories: day nests (daytime retreats), breeding nests (places for nursing the young), pre-hibernation nests (during preparations for hibernation) and hibernation nests (places for actual hibernation). Construction materials and nest locations were also documented. Nesting behaviour was studied by analysing changes in the numbers of nests and in the nest change frequency. In addition, the frequencies of sequential nest use, resting without a nest and the proportion of each nest type observed in different habitats were studied. In order to estimate spatial patterns of nest usage and nesting habitat use, the geographical locations of the nests were included in a home-range analysis (I, II). The numbers of nests in the K50 area, outside the K95 area (active locations included) and in the part of the home range overlapping with a neighbour's K95 and/or K50 were also analysed.

2.5 MORTALITY, DISEASES, PARASITES AND DIET

To study mortality, diseases and diet, hedgehog carcasses were collected from the area during the radio telemetry study and local people were invited by means of a newspaper advertisement to collect dead specimens for examination (III; Fig. 1A). Traffic mortality among hedgehogs was studied by driving along a 46-km survey route three to four times a week from May to October (altogether 5,656 km in summers 2004 and 2005) (Fig. 1A). The carcasses were stored at -20°C for further examination.

Human-related and natural mortality factors were studied from collected carcasses (n=253) (III). These enabled seasonal patterns of traffic mortality and the proportions of hedgehogs found dead on different sections of the roads to be analysed.

Post mortem examinations (*n*=38) were performed to determine diseases, parasites, bacteria and the cause of death in cases of carcasses with signs of disease or an unknown cause of death (III). Necropsy included gross pathology, inspection for endoparasites and histology for fresh carcasses. Bacteriological aerobic cultures were performed on the lung, liver and small intestine and other tissues if necessary. Anaerobic cultures were also performed when necessary. *Salmonella* enrichment was performed on the intestine and liver, with serotyping of the isolated *Salmonella* strains. Muscles tissues were tested for *Trichinella* spp. Ticks were identified by their morphology under a microscope and with reference to the literature.

Only the carcasses with an undamaged stomach were included in the dietary investigation (*n*=33), the stomach being removed as soon as possible after discovery (III). Diet was studied by identifying the undigested food items and hard parts in the stomach contents. All food items were identified to the lowest possible taxonomic level using the literature and reference collections. Differences in food composition between the sexes and age groups were studied.

2.6 METAL AND METALLOID CONCENTRATIONS AND AGE DETERMINATIONS

Tissue samples (kidney, liver, hair and spine) for metal analyses were collected mainly from the animals killed on roads, but the group also included juveniles that had starved to death (altogether 65 carcasses) (IV). The tissue concentrations of the metals cadmium (Cd), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), molybdenum (Mo), nickel (Ni), lead (Pb) and zinc (Zn), and the metalloids arsenic (As) and selenium (Se) were analysed. Reference material and blanks were included in the element determination procedure for quality assurance purposes.

Sex and age-based differences in metal and metalloid concentrations in the tissues were studied (IV), as also were the concentration differences between tissues and relations of metal and metalloid concentrations within specific tissues.

The age of each hedgehog was determined from a transverse section of the lower jaw (IV). The jaw was fixed in neutral formalin, decalcified, dehydrated and embedded in paraffin, and was then cut into thin sections and stained. The age of each individual was calculated from the periosteal growth lines in the bone, with each line representing 1 year (Fig. 2).

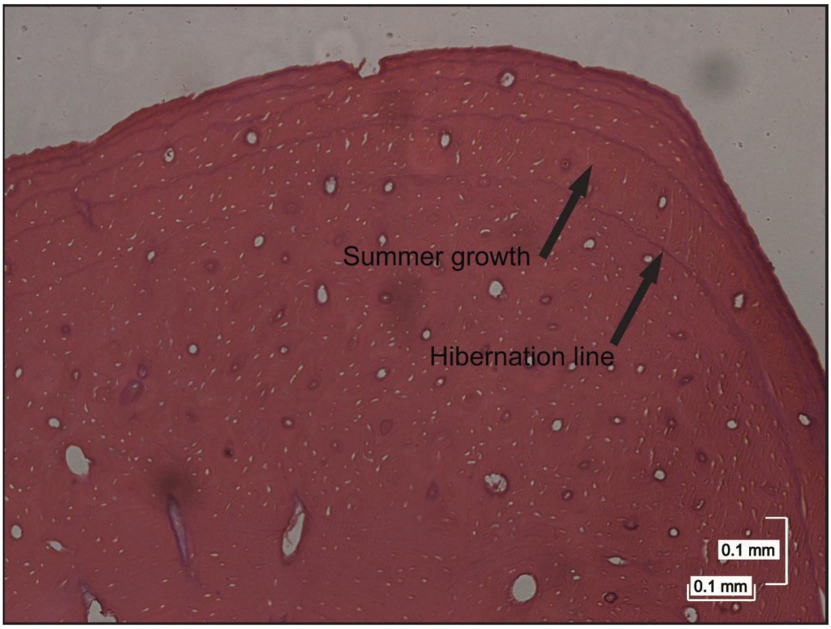

***Figure 2**. The age of hedgehog was calculated from the periosteal growth lines of lower jaw section. This individual was five years old.*

2.7 STATISTICAL ANALYSES

Linear mixed effect models, general estimating equations and multivariate analysis of variance (MANOVA) were used to test sex and age-related differences in home-range size and overlap, number of nests, nest change frequency, number of nests overlapping with home range of other individuals and concentrations of metals and metalloids (I, II, III, IV).

After MANOVAs, linear regressions were performed to investigate the relationship of metals and metalloids and age (IV). Friedman's tests were used to compare the concentrations of each metal, As and Se among tissues, Wilcoxon's signed-rank tests were conducted to evaluate which tissues differed from each other in their concentrations and Spearman's rank correlations were calculated to study the relations between concentrations.

Fisher's exact tests were conducted to test the differences between sexes in frequencies of different nesting behaviour and to assess differences in the frequency of road deaths (II, III). Chi-square tests were performed to study differences in the frequency of road deaths between seasons, sexes and between the road sections (III). Permanova+ routine was used to examine sex and age related differences in food composition (III).

The following software packages were used for the statistical analysis (I, II, III, IV): R 2.15.0 (R Development Core Team 2012), SPSS 16.0 and 19.0 for Windows (SPSS Inc., Illinois, USA) and Primer-E (Anderson et al., 2008). More specific details of the materials and methods can be found in the original papers.

3 Results and Discussion

3.1 MOBILE HEDGEHOGS

Hedgehogs move over a wider area and have a greater number of nests at northern latitudes than they do in more temperate areas (Reeve, 1982; Boitani & Reggiani, 1984; Kristiansson, 1984; I; Fig. 3). Increasing latitude (>50°N) is broadly associated with decreasing primary productivity (Huston & Wolverton, 2009), and mammals living in less productive habitats generally have larger home ranges, since they have to move over greater distances to find food (Harestad & Bunnell, 1979; Damuth, 1981; Dahle & Swenson, 2003; Kauhala et al., 2005).

In Finland, where the hedgehog is living on the northern edge of its distribution range, the growing season is only 130-175 days, whereas in southern Europe it is over 225 days (Rötzer & Chmielewski, 2001; Tveito et al., 2001; Karlsen et al., 2006). Thus the annual active period is very short and individuals have less than five months in which to breed and prepare for the coming winter (I, II). The length of the active period and the allocation of energy to reproductive and non-reproductive activities differs over the species' distribution range, so that in Italy, for example, hedgehogs can be active from March until December (Boitani & Reggiani, 1984) whereas in Finland, their active period is from the end of April until September-October (I, II). Kristiansson (1984) divided the period of activity into the mating season and post-mating season, but our results showed that the post-mating season could be further divided into two parts: a post-mating season for fat storage and a pre-hibernation season as a transition to hibernation, although fat storage also continues (I, II).

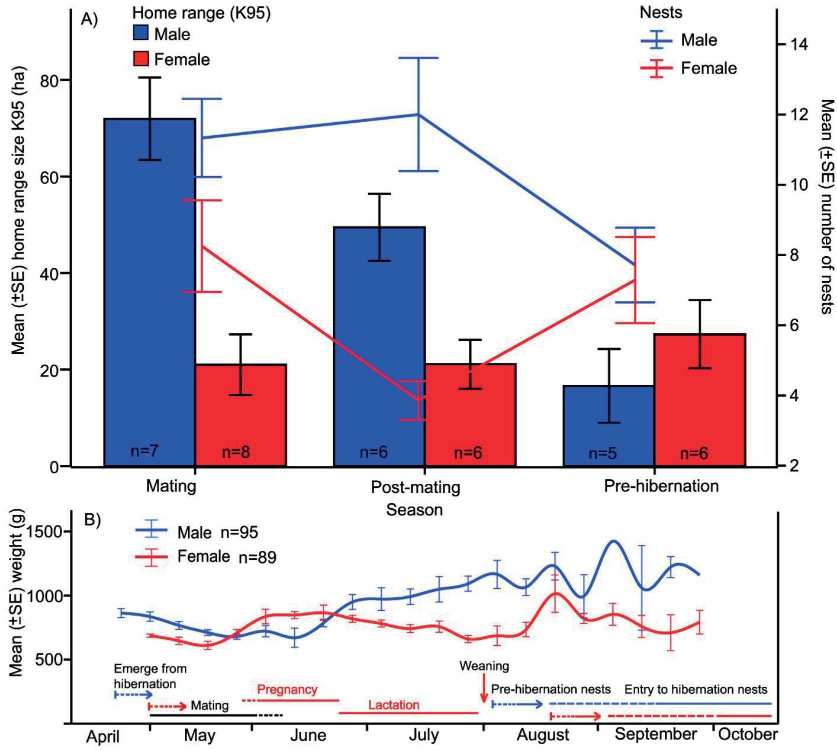

Figure 3. A) The home-range size (K95), number of nests (mating season; males n=6, females n=8, post-mating season; males n=6, females n=7 and pre-hibernation season; males n=5, females n=6) and B) weight fluctuation of hedgehogs during the active period.

3.2 THE SOLITARY HEDGEHOG – DIFFERENT MOVEMENT PATTERNS FOR THE SEXES

By operating over a large home range during the mating season (K95 average 72 ha), the male ensures contact with as many females as possible (Boitani & Reggiani, 1984; Kristiansson, 1984; I; Fig. 3A). Males also expressed the widest variety of nesting behaviour in mating season, including a high number of nests per individual, different males used the same nest sequentially and males rested at times without a nest (II). By contrast, the female's home range was clearly smaller (K95 average 21 ha) (I;

Fig. 3A). In general the movements of the sexes are related to their different reproductive strategies within the promiscuous mating system, in that the females allocate energy to pregnancy and nursing, whereas the males concentrate on finding females and do not participate in parental care (Moran et al., 2009; Kristiansson, 1984; Riber, 2006; I). Both sexes mate with several partners (Kristiansson, 1984; Jackson, 2006; I). The overlaps in home ranges with several individuals of both sexes observed here are consistent with the promiscuous mating system found in this species (Steinmann et al., 2005; Jackson, 2006; Blondel et al., 2009; I).

The mating season began soon after emergence from hibernation and lasted only four to five weeks (I, II), whereas further south it lasts from two to four months (Kristiansson, 1981; Jackson, 2006). The males emerge earlier than the females, in order to be ready to find mates as early as possible (Göransson et al., 1976; I, II). The male sexual cycle varies regionally, and in Fennoscandia testis activity starts in January, during the hibernation period, with maximum testosterone secretion and spermatogenesis occurring in May (Reeve, 1994). Hedgehogs in Finland may have a higher cold tolerance than German hedgehogs, which retire to their winter nests at higher ambient temperatures than do the Finnish ones (Kristoffersson & Soivio, 1967). This cold tolerance, combined with early testosterone secretion, means that the males are ready for mating in early May despite of the continued low ambient temperatures (Kristoffersson & Soivio, 1967).

The females nursed their offspring in breeding nests several weeks around midsummer, a time when home ranges remained small (K95 average 20 ha), their core areas were at their smallest and the number of nests used was lower than at other seasons (Fig. 3; I, II). The lactation period limits the home range of other small mammals (Koskela et al., 1997). Females sometimes rested without a nest, probably due to the increased daily activity resulting from the need for extra nutrition brought about by lactation or just a desire to retire in peace out of reach of their young (II). The high ambient temperatures around midsummer may also lead to behaviour of this kind.

Females avoided each other (I). Home ranges (K95) of hedgehogs overlapped, except female-female core areas (K50) after the mating season (I; Fig. 1B). Exclusive space use by the females may be attributed to avoidance of same-sex individuals rather than the defending of a territory. According to Riber (2006) and Haigh (2011) female ranges do not overlap or overlap only slightly. Hedgehogs are not territorial (Reeve, 1982; Boitani & Reggiani, 1984; Riber, 2006), but mutual avoidance of individuals (Morris, 1969) or retention of a personal feeding space is suggested (Cassini & Föger, 1995). We found no nests in the core areas of other females (II) and females have rarely been found to inhabit a nest used earlier by another female (Haigh et al., 2012; II), although they may sometimes use a nest that had previously belonged to a male (II). Exclusive space use by females also takes place in other small mammals (e.g. Ostfeld, 1990; Wolff, 1993; Blondel et al., 2009). Overall, home ranges overlap, but individuals may not use the same area simultaneously (I; Morris, 1969). However, in feeding sites avoidance of other individuals is usually impossible and fights are common.

After weaning the juveniles, the females actively searched for food over a wider area (K95 average 29 ha) and started to accumulate fat reserves in preparation for hibernation (I; Fig. 3). The movements of males, on the other hand, clearly decreased after the mating season (K95 average 48 ha), although numerous nests were constructed and changed frequently, indicating that they were concentrating on foraging for the rest of the active period (I, II; Fig. 3A). The fact that the centre of the male home range shifted during the active period indicates that mating and foraging take place in separate areas (I). The home range was smallest in late summer (K95 average 17 ha), when the males started to prepare themselves for hibernation, and the number of nests used also decreased at that stage.

3.3 THE GREAT IMPORTANCE OF NESTS

Nests are especially important for hedgehogs in northern areas, since they spend 85% of their time every year in a nest (II), for in addition to the long hibernation period, they spend more than half of the day in a nest at other times. The hedgehogs in Joensuu stayed in their hibernation nests for an average of 223 days, the longest hibernation period reported anywhere in the species' distribution range (Kristiansson, 1984; Jensen, 2004; II).

Hedgehogs have four different types of nests in northern areas (II), rather than the three found earlier (Morris, 1973; Reeve, 1994; Haigh et al., 2012). The new type described here was the pre-hibernation nest used for preparing for overwintering (II). This could also serve as a backup if the real hibernation nest were to be destroyed. The male hedgehogs used an average of 24 nests during the active period (changing 30 times), whereas the females had 17 (changed 26 times). Males generally have more nests than females, and also change nests more often (Reeve & Morris, 1985; Haigh et al., 2012).

3.3.1 Residential areas – summer nesting habitats

For nesting purposes, the hedgehogs needed diversified residential areas that often bordered on forest (II). Gardens that include features such as shrubs, wood piles and sheds attract hedgehogs and are suitable day nesting sites (Hof & Bright, 2009; II). The presence of structurally complex vegetation is suggested to be more important than the species composition of the vegetation in predicting the occupancy of urban sites by small mammals (Garden et al., 2007). The most typical nest construction materials were leaves, grass and twigs, and availability of these materials in gardens was of benefit to the hedgehogs (II). There is a trend nowadays to tidy up gardens, however, which means that there are increasingly less sheds and woodpiles in gardens and most of the suitable construction materials have been carefully tidied away. This reduces the suitability of gardens as habitats for hedgehogs, as also for other small to medium-sized mammals.

The presence of a nesting box in a garden attracts hedgehogs (Hof & Bright, 2009), but nesting boxes were used by adult individuals on only a few occasions (II). Nests made by humans may not be important for adult hedgehogs, although they can be useful for juveniles, for example, or as occasional resting places for adults (Riber, 2006; II).

3.3.2 The significance of forests as overwintering areas

Hedgehogs need natural areas such as forests for hibernation (Jensen, 2004; II). Thus the pre-hibernation and hibernation nests were often in coniferous forests and were more thoroughly constructed than the day nests and situated typically under tree roots or burrowed into moss tussocks (II). The hedgehogs had a clear transition period in late summer marked by nesting habitat change and the construction of pre-hibernation nests, something that is probably more pronounced at higher latitudes. At this stage they moved away from the built-up areas into the forest, where there is less human activity, the heaviest males doing so as early as the beginning of August. The females moved to the overwintering areas more than two weeks later than the males.

Similar seasonal movements just before hibernation have been observed in Great Britain and Ireland (Morris, 1969; Morris, 1973; Haigh, 2011). The notable proportion of male hedgehog nests outside the individual's active home range in the pre-hibernation season was indicative of this change (II). During the transition period activity was concentrated in the overwintering areas, where new nests were constructed and individuals remained mostly in their nests during the night as well, so that movement and foraging decreased. These features may be related to the spontaneous bouts of transient shallow torpor experienced at the onset of hibernation (Fowler & Racey, 1990). The function of these bouts is unclear, but they may indicate physiological preparation for hibernation or further energy conservation. Testosterone levels also decrease rapidly in the males in autumn, an effect that plays an important regulative role in hibernation, whereas in the females hibernation is mainly linked to changes in ambient temperature and food availability

(Pfäffle, 2010). The male hedgehogs hibernated from August-September until April and the females from September-October until May (I, II).

3.4 HEAVY NORTHERN HEDGEHOGS

The hedgehogs were slightly heavier than those described in more temperate climates (Boitani & Reggiani, 1984; Parkes, 1975; Kristiansson, 1984; I). Male hedgehogs are in general heavier than females (Haigh et al., 2012; I; Fig. 3B), which provides some evidence of sexual dimorphism, although species with a promiscuous mating system usually tend to show only little or no sexual dimorphism (Heske & Ostfeld, 1990). During the mating season the males moved a lot and spent a great deal of time looking for females, so that their body weight decreased (spring average 755 g; I; Fig. 3B). Males can survive short-term starvation during the mating season (Kristiansson, 1984). After an intense mating season the males start to accumulate fat reserves, and their weight increases for the rest of the active period (midsummer average 900 g; I; Fig. 3B). The males were heaviest just prior to hibernation (average 1117 g).

The females' weight variation was related to pregnancy and nursing their offspring in the course of the active period (I; Fig. 3B). Their body weight decreased during mating season (average 667 g) but increased during pregnancy until they gave birth, and lactation again reduced their weight (midsummer, average 794 g). After weaning their young they therefore had to increase their body weight within a very short time to survive the coming long winter hibernation. Average weight for females prior to hibernation was 790 g. The weight variation seen here in both sexes during the active period was in accordance with previous reports (Kristiansson, 1984; Reeve, 1994), their average weight loss during hibernation being 28% (I), as compared with 20-40% elsewhere in northern Europe (Kristoffersson & Suomalainen, 1964; Kristiansson, 1984; III). Further south, where the hibernation period is shorter, weight losses of 3-38% have been quoted (Haigh et al., 2012).

3.5 TRAFFIC AND HEDGEHOGS – BUMPS IN THE NIGHT

The hedgehog was in Joensuu the most typical small mammal killed on the roads (III). Anthropogenic factors such as traffic have a distinct effect on hedgehog mortality: in the Netherlands, for instance, traffic mortality may be high enough to affect hedgehogs at the population level, since 113 000-340 000 hedgehogs are killed on the roads each year (Huijser, 2000).

In Joensuu, the number of hedgehogs killed per 100 km of road transect was 0.65 (III). By comparison, 6.4 per 100 km were killed in New Zealand (Morris & Morris, 1988) and 0.26 per 100 km in Ireland (Haigh, 2011). The roads concerned in these recent studies represented a wide variety of environments (Morris & Morris, 1988; Haigh, 2011), whereas our survey route was entirely within a built-up area of the kind considered previously to entail a higher risk of hedgehogs being killed by traffic (Göransson et al., 1976; Orlowski & Nowak, 2004). The low number of hedgehog deaths recorded here may be related either to the lower hedgehog density than in areas with a more temperate climate or to the lower traffic intensity (III). Neither the habitat type nor the speed limit zone had any effect on the frequency of deaths, the highest frequencies were found in the survey route's most typical habitat type (gardens) and most common speed limit zone (30-40 km/h).

Hedgehog mortality on the roads was most common in July-August (III). Adult females were killed by traffic especially in late summer, a time when they extend their home range after weaning the juveniles (I, III), while juveniles themselves were regularly found dead on the roads in August-September, having began their independent life in late July or early August (III). There was no difference between the sexes in the frequency of road deaths (III), unlike the situation in earlier studies, where males were found to be more vulnerable to accidents of all kinds and traffic mortality was high during the mating season (Göransson et al., 1976; Huijser, 2000; Haigh, 2011).

The natural mortality factors mainly included starvation in the case of juveniles and purulent, gangrenous inflammation of the limbs in adult males (III). Starved individuals were found from August onwards, having also been weakened by endoparasites (III). Purulent, gangrenous inflammation of the feet occurred during one mating season and affected only adult males (III), the cause having most probably been scratch and bite wounds gained in fights.

3.6 A CARRIER OF PARASITES

Over 90% of the carcasses examined had parasites (III). The high prevalence of parasites generally found in hedgehogs may be a possible factor in the population declines observed in Great Britain (Gaglio et al., 2010). Parasites can limit the energy invested by the hedgehog in growth, fat storage or immunological reactions (Pfäffle, 2010).

3.6.1 Endo- and ectoparasites

Most of the hedgehogs had lungworms (*Crenosoma striatum*) (III), which is a very common endoparasite of this species (Huijser, 2000; Egli, 2004; Gaglio et al., 2010), causing bronchitis and bronchopneumonia (III). *Capillaria* spp. occurred only in the intestines, and caused enteritis (III). *Capillaria* spp. infection probably has a major effect on morbidity and on survival at times of high stress such as mating or hibernation (Pfäffle, 2010). *Capillaria spp*. and *Crenosoma striatum* are acquired by ingesting infected hosts (e.g. earthworms, snails) (Majeed et al., 1989).

Endoparasites were more abundant in the juveniles than in the adults (III) as observed also by Reeve & Huijser (1999) whereas Majeed et al., (1989) suggested that the probability of infection increases with age. The low prevalence found here in adults may be the result of acquired immunity or of increased mortality in infected individuals (Poulin, 2007). Parasites can be a major threat for a juvenile whose immune system is not fully developed (Pfäffle, 2010). High infection rate in recently weaned juveniles can explain the high rate of starved juveniles (III).

Nearly half of the adult hedgehog carcasses examined had ticks (*Ixodes ricinus*) (III) that is the most important vector of *Borrelia burgdorferi* s. l. and the tick-borne encephalitis (TBE) virus throughout Europe (Skuballa et al., 2007; Andreassen et al., 2012). Hedgehogs harbour at least three *Borrelia* genospecies, all of which are known to be (*B. afzelii*, *B. bavariensis*), or are strongly suspected of being (*B. spielmanii*), pathogens for humans (Skuballa et al., 2007; 2012; Wilske et al., 2007). The average rates of *B. burgdorferi* s.l. infections in the ticks of the built-up areas of southern Finland have been 5-32% (Junttila et al., 1999; Mäkinen et al., 2003). In hedgehogs high tick prevalence may cause blood loss that can lead to anaemia (Pfäffle et al., 2009). Chronic tick-induced blood loss may have effect to sick, young and old animals and may be particularly important for animals entering hibernation or just leaving hibernation (Pfäffle et al., 2009) since this is a period of severe physical stress (Heldmaier et al., 2004).

Nests are thought to be the places where ectoparasites spread (Brinck & Löfqvist, 1973; Philpot & Bowen, 1992; Reeve, 1994), and at least some parasites are probably already transmitted to juveniles in their breeding nests (Brinck & Löfqvist, 1973). Adult hedgehogs in turn also use the same nests and this behaviour may promote the spread of parasites from one individual to another (Reeve & Morris, 1985; II; III).

3.7 AN OMNIVORE HEDGEHOG

Although the hedgehog's insectivorous diet consisted of invertebrates such as beetles (Coleoptera) and earthworms (Clitellata), also vertebrates and plant material were commonly eaten (III). The natural part of diet seems to be rather similar through the species' distribution range, although each region has its own particular spectrum of prey items (Reeve, 1994; III).

Juveniles are inexperienced as predators, and thus utilize what is available, e.g. food offered by humans, slow-moving spider species, and vertebrate carrions, but adult hedgehogs are more skilled and have a wider prey repertoire (Yalden, 1976; Dickman, 1988; III). *Trichinella* was not observed in any of the hedgehog carcasses, but the hedgehog is a potential host (Famerée et al., 1982), since it feeds on vertebrates or their carrion.

Just as our hedgehogs took advantage of the food resources available, including food provided by humans (III), so Hof & Bright (2009) also observed that extra food sources in gardens attract hedgehogs. They can benefit from supplementary food that is rich in calories, and this is probably more pronounced at northern latitudes, where fat reserves for winter hibernation have to be gathered in very short space of time (III). Supplementary feeding is especially prominent in urban and sub-urban areas, since plenty of food is made available, both intentionally and unintentionally (Prange et al., 2004; Hubert et al., 2011).

There are also negative side–effects, however, when hedgehogs gather at feeding sites (III). Since the hedgehog is mainly a solitary animal mutually avoiding each other, except during the breeding and nursing season (I; II), the presence of several individuals at the same feeding site constitutes an unnatural situation and fights between individuals occur (III). The high incidences of *Salmonella* and bacterial wound infections observed here cast doubts on the necessity for feeding hedgehogs and on the state of hygiene at feeding sites. Zoonotic diseases such as *Salmonella* spread via faeces from one hedgehog to another and from hedgehogs to humans (Keymer et al., 1991; Handeland et al., 2002; Nauerby et al., 2000). In the present case 57% of the hedgehogs examined had a *Salmonella* Enteritidis infection, often in latent form in the liver (III). Unsuitable food items such as cows' milk offered at feeding sites may contribute to the development of latent salmonellosis into active shedding of bacteria in the faeces (Keymer et al., 1991).

The generally flexible behaviour of hedgehogs reduces the likelihood of undue dependence on artificial food, and it is thus treated as a supplement to natural food and not a replacement for it (Morris, 1985). For that reason a discontinuation of feeding at times when natural food is easily available will not do any harm to hedgehogs but, on the contrary, may reduce the negative side-effects of supplementary feeding (III). Hedgehogs benefit most from artificial feeding during the late summer and autumn, when they are gathering their fat reserves.

3.8 CONCENTRATIONS OF METALS

The concentrations of heavy metals such as cadmium (Cd) and lead (Pb) measured in our comparatively unpolluted urban area were generally lower than those measured in hedgehogs and other small mammals earlier in more polluted areas (Hunter et al., 1989; D'Havé et al., 2006; Komarnicki, 2000; Pankakoski et al., 1993). The mean kidney Cd concentration in the present material, for example, 5.74 µg/g dry weight, was well below the figure of 45 µg/g dry weight quoted earlier for hedgehogs (D'Havé et al., 2006) and way below the concentration of 350 µg/g dry weight which is thought to cause tubular dysfunction in small mammals (Cooke & Johnson, 1996). Similarly, the mean kidney Pb concentration (0.95 µg/g dry weight) was below that measured earlier in hedgehogs, 5 µg/g (D'Havé et al. 2006) and well below the figure of 15 µg/g taken as indicative of Pb toxicosis in mammals (Ma, 1996). Heavy metals such as Cd and Pb have no biological function and are highly toxic, and Cd has good mobility through the food chain (Ma & Talmage, 2001). Mean liver concentrations of the essential elements copper (Cu 18.53 µg/g dry weight) and zinc (Zn 228.97 µg/g) were also lower (IV) than those measured earlier in hedgehogs (Cu 64 µg/g, Zn 371 µg/g; D'Havé et al., 2006). Results showed that average pollution levels of a random sample of hedgehogs in Joensuu are low (IV). No information is available on the concentration of selenium (Se) in hedgehogs, but the mean liver Se concentration in the present material (2.40 µg/g) was higher than measured in California voles (*Microtus californicus*), 1.56 μg/g (Clark, 1992).

3.8.1 Distribution of metals and metalloids in tissues

The distribution of metals and As in tissues was similar to that found in hedgehogs earlier (D'Havé et al., 2006), e.g. nickel (Ni) was mainly stored in the hair and Cd in the liver and kidney (IV). No information is available on the tissue distribution of Se in hedgehogs. Apart from Mo, notable concentrations of metals, As and Se can also be detected in the external tissues, i.e. the hair and spines (D'Havé et al., 2006; Vermeulen, 2009; IV). The use of external tissues can enable metals to be monitored in live animals as well. Spine moulting is probably a continuous process, while only little is known about hair moulting in hedgehogs (Reeve, 1994). The hair is in constant contact with the blood stream during growth and incorporates many pollutants from the blood, thereby reflecting long-term exposure (Henderson, 1993).

Concentrations were usually higher in the internal organs, but Cu and Ni were highest in the hair and As concentrations at the same level in all tissues (IV). Arsenic is gathered first into the liver and kidney, while later the majority of it is excreted into the urine and transported to the external tissues (Vahter, 1994). The high concentration of Cu in the hair may also be a consequence of the involvement of this metal in structural proteins and hair pigmentation (Hunter et al., 1989).

3.8.2 Accumulation with age

There was a strong tendency for cadmium to accumulate in the tissues of hedgehogs with age, indicating that heavy metals can accumulate in the tissues of this quite long-living animal even in fairly unpolluted environments (IV). Food of insectivores is more seriously contaminated than that of rodents (Ma & Talmage, 2001). The hedgehog runs a risk of metal intoxication (Alleva et al., 2006; D'Havé et al., 2006). Earthworms form part of the hedgehog's natural diet (III) and these are known to accumulate high levels of metals (Ma et al., 1991; Lukkari et al., 2004). Accumulation of Cd with age has been observed earlier in other insectivore species such as the mole (*Talpa europeaus*) (Pankakoski et al., 1993; Komarnicki, 2000) and the common shrew (*Sorex araneus*) (Hunter et al., 1989).

Age-related accumulation of selenium (Se) and molybdenum (Mo) were also observed (IV), even though the natural concentration of Se in the soil is low in Finland, so that it has been added to fertilizers since the 1980s (Arthur, 2003). Selenium has a tendency to counter or eliminate the toxic effects of Cd (Wlodarczyk et al., 1995), and increased dietary levels of Mo and sulphur (S) were observed to reduce the accumulation of Cd in the tissues of sheep (Smith & White, 1997). Common shrews may be more tolerant of Cd than are rodents, on account of their ability to store it in a non-toxic form (Shore & Douben, 1994). The detoxification mechanisms employed by hedgehogs against heavy metals may have also developed further during evolution than those of most other terrestrial mammals, because it can be assumed that the species was exposed to a risk of metal toxicity through to its natural diet even before the era of human-inflicted pollution (IV). The increases in Mo and Se concentrations already observed here after the accumulation of comparatively low amounts of Cd may be connected with this. Also, the long hibernation period in northern areas may protect hedgehogs from metal loads, since their metabolism is lowered at that time (IV) and since Cd, for example, is bound to proteins instead of the fat reserves used during hibernation (Underwood & Suttle, 1999). Actively wintering small mammals are forced to increase their food intake under cold conditions.

Based on the present findings and those of earlier studies, hedgehogs can be used as bioindicators of metal pollution in urban and sub-urban areas (D'Havé et al., 2006; Vermeulen, 2009; IV). As a small mammal, the hedgehog has a fairly restricted home range, so that pollutant concentrations at the population level tend to reflect local pollution (D'Havé et al., 2006; Vermeulen, 2009). It is also a relatively accessible animal for research purposes and quite long–living, up to seven years in the present material (IV), so that individuals may reflect relatively long-term exposure to contaminants of a kind that could result in chronic toxicological effects (D'Havé et al., 2006; Vermeulen, 2009).

3.9 IMPLICATIONS FOR CONSERVATION AND FUTURE RESEARCH

Hedgehog population has declined in the Great Britain and Central Europe (Huijser, 2000; Hof, 2009; Dowding, 2007). There is also a common impression among people in Finland that hedgehogs are seen less frequently nowadays (Karlsson, 2001; Koskinen, 2012; Nyström & Kinnunen, 2013). Hedgehog distribution in Finland has been studied previously (Kristoffersson et al., 1966; 1977; Terhivuo, 1990), but the size of the population has never been estimated. A monitoring programme would be required to determine the current distribution and size of the Finnish hedgehog population for identifying trends and potential risks for the species.

This thesis provides novel information about hedgehog's behavioural ecology, but more precise data is still needed in order to ensure their protection now and in the future. The new research equipment currently available, including microGPS-dataloggers, should give us more precise data (Recio et al., 2013), but up to now these loggers have been too heavy for small mammals such as the hedgehog.

An important aspect for hedgehog conservation is to maintain diversity in residential areas and retain patches of semi-natural and natural vegetation in urban and sub-urban areas. Habitat fragmentation probably is one of the reasons for the decline in this species, as connectivity is important for its movement and the occurrence of green spaces such as parks, commons and woodlands is positively related to its presence in an area (Hof, 2009; Hof & Bright, 2009). For that reason there is little use in conserving patches of natural vegetation if the distance between the patches is too great or they are separated by wide, heavily used roads.

Climate change may be a significant factor affecting the survival and distribution of animal species in the future, as it has been predicted that in Finland annual mean temperature will rise, temperature will rise more in winter than in summer and summers continue to become hotter (Jylhä et al., 2009). Also precipitation is projected to increase and heavy rain events to intensify. Hedgehog is not the most vulnerable species compared to arctic species and may even benefit from lengthen of growing season and extend its distribution further north as the climate becomes warmer. However, substantial temperature or precipitation changes in the middle of the winter are likely to interfere with hibernation.

More information is needed about the effects of *Salmonella* infections on hedgehogs and their role as a source of *Salmonella* infection in humans. In addition the costs and benefits of supplementary feeding should be estimated. Similarly, the role of hedgehogs in maintaining local tick populations in urban areas should be studied further. Ticks have extended their distribution and increased in abundance over recent years (Scharlemann et al., 2008), and they may become more abundant in certain regions if the climate becomes milder (Lindgren et al., 2000).

Although this thesis demonstrates seasonal patterns of traffic mortality and the proportions of hedgehogs found dead on different sections of the roads, the influence of traffic mortality on hedgehog populations in Finland is still unknown. Traffic signs that warn about small mammals and an increased use of speed bumps, or "sleeping policemen", on roads passing through residential areas could substantially reduce traffic mortality among small mammals. Speed bumps force drivers to slow down and effectively reduce night-time speeds, making it easier to detect animals coming onto the road.

The monitoring of concentrations of environmental pollutants in hedgehogs would also be important in view of the risk of the age-related accumulation of heavy metals. In addition, it will be important to consider that there are many more pollutants than heavy metals that act upon wildlife, resulting in complex mixture toxicity effects (D'Have, 2006).

4 Conclusions

The following conclusions can be drawn from this study of the behavioural ecology of the hedgehog in built-up areas at the northern limit of its distribution range:

1. Hedgehogs have a wider home range and a greater number of nests when living in harsher climates and less productive areas. Heavy northern hedgehogs save energy by hibernating through the harsh winter and do so for longer than in any other area. Although hedgehogs are not territorial, females avoid each other. Overall, the results indicate a flexible assimilation of the hedgehog's behavioural ecology to different habitats and climatic conditions.
2. Nests are important for the survival of hedgehogs at northern latitudes, since they spend most of their time annually in nests. The hedgehog needs diverse residential areas for nesting purposes, but semi-natural and natural areas such as forests are also needed, especially for overwintering.
3. Hedgehogs were the most typical small mammal to be found dead on the roads of the area studied here, the frequencies of their road deaths being highest in July-August. Typical natural cause of death was starvation of juveniles. Hedgehogs also suffer from a high prevalence of ecto- and endoparasites.
4. Hedgehogs utilize variety of opportunistic food items in urban habitat. Diet consists mainly of invertebrates, but hedgehogs also consume extra food resources such as milk and fish. They benefit from supplementary food, but there are also negative effects that have to be considered. Infections such as *Salmonella* and various parasites may be transmitted from one individual to another at feeding sites, and also to humans.
5. The hedgehog can be used as a bioindicator of metal pollution. The current pollution load in present material was not a cause for concern, but there is a clear tendency for hedgehogs to an age-related accumulation of heavy metals through their invertebrate diet.

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