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MARJA NIEMI

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– implications for conservation

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Author's address: University of Eastern Finland
Department of Biology
P.O.Box 111
80101 JOENSUU
FINLAND
email: marja.niemi@uef.fi

Supervisors: Senior researcher Mervi Kunnasranta, Ph.D.
University of Eastern Finland
Department of Biology
P.O.Box 111
80101 JOENSUU
FINLAND
email: mervi.kunnasranta@uef.fi

Professor emeritus Markku Viljanen, Ph.D.
University of Eastern Finland
Department of Biology
P.O.Box 111
80101 JOENSUU
FINLAND
email: markku.viljanen@uef.fi

Professor emeritus Ismo J. Holopainen, Ph.D.
University of Eastern Finland
Department of Biology
P.O.Box 111
80101 JOENSUU
FINLAND

Docent Hannu Huuskonen, Ph.D.
University of Eastern Finland
Department of Biology
P.O.Box 111
80101 JOENSUU
FINLAND
email: hannu.huuskonen@uef.fi

Reviewers: Professor Brendan P. Kelly, Ph.D
Division of Polar Programs
National Science Foundation
4201 Wilson Blvd, Suite 755
ARLINGTON, VIRGINIA 22230
USA
email: bkelly@nsf.gov

Senior Curator Olle Karlsson, Ph.D
Department of Environmental Research and Monitoring
Swedish Museum of Natural History
BOX 50007
Se-104 05 STOCKHOLM
SWEDEN
email: Olle.Karlsson@nrm.se

Opponent: Professor Eero Helle
Finnish Game and Fisheries Research Institute
P.O.Box 2
00791 HELSINKI
FINLAND
email: eero.helle@rktl.fi

ABSTRACT

More knowledge of the behavioural ecology of the Saimaa ringed seal (*Phoca hispida saimensis*) is urgently needed for effective conservation of this critically endangered subspecies. The seal population of Lake Saimaa in south-eastern Finland is threatened by several anthropogenic impacts, especially the high mortality caused by juvenile by-catch. In order to provide scientific data to support conservation measures, free-ranging Saimaa ringed seals in central Lake Saimaa were studied using various tracking techniques such as audiovisual monitoring and VHF and GPS telemetry. Also, spatial data on the lairs and habitat usage of the seals were used to estimate the current distribution and breeding area of the Saimaa ringed seal and to identify nursing sites.

This is the first time that the behavioural ecology of Saimaa ringed seal pups has been studied. The natal sites were found to be still actively used by both the pup and the mother in April, although the sheltering snow lair had melted. By this time the mother and pup were communicating vocally. The average size of a pup's home range during the nursing season in April–May was 2 km^2. The pups dispersed from their natal sites in mid-May on average. They explored wide areas, so that their maximum distances from their natal sites were already 3–25 km by the end of June, at an age of ca. 3–4 months.

This study revealed new information on the haul-out and movements of Saimaa ringed seals and on their responses to outboard motorboat traffic. During the moulting season in May–June the hauled out seals were alerted by an approaching outboard motor boat at an average distance of 240 m. At the distance of ca. 150 m the seals entered the water. The adults and pups had total home ranges of a similar size (averaging ca. 90 km^2), although the methodological differences between GPS and VHF tracking may have affected the results by underrating the home range sizes. Also, the adults' home ranges were more stable and they showed a more sedentary pattern of life, making only a few sporadic movements, whereas the pups continued to explore their habitat during their first year. In addition, the adults had an average of 13 haulout sites during the open-water season, about half of which, situated mostly on the eastern or southern shores of small islands, were used intensively. After the moult the seals mostly hauled out nocturnally. Single haulout event lasted 6 ± 5 h (mean ± SD).

The seals' current distribution and breeding areas covered ca. 70% and 51% of Lake Saimaa, respectively. The knowledge gained in this thesis should be of value to conservation practitioners and decision-makers when planning fishing restrictions, sustainable land usage on the shore and guidelines for tourism in order to mitigate disturbance to the seals and by-catch.

Universal Decimal Classification: 574.2, 574.9, 591.52, 591.582, 599.745.3

CAB Thesaurus: Phoca hispida; seals; pups; animal behaviour; habitats; breeding places; nests; conservation; spatial distribution; movement; tracking; telemetry; vocalization; Finland

Yleinen suomalainen asiasanasto: saimaannorppa; poikaset; habitaatti; eläinkannat; elinpiirit; lisääntyminen; liikkuminen; seuranta; pesät; äänet; suojelu; Saimaa; Suomi

Preface

Like the old poet Donne wrote, “no man is an island”, well, neither is a PhD student working with Saimaa ringed seals. There are so many people who have been encouraged and helped me during this work; here are only the few of them. First of all, my sincerely appreciation goes to all of my supervisors, the present and the former; Jouni Taskinen for the opportunity to begin to study Saimaa ringed seals, Ismo Holopainen for all the support on this research and thesis, Markku Viljanen for the strong influence behind the project by helping especially with the funding and Hannu Huuskonen for the encouragement on this thesis. Last but not least, I would like to express my deepest gratitude to my principal supervisor Mervi Kunnasranta, who has been there all the way and without whom this project would have not ever been possible. With her devoted enthusiasm for the subject and determined guidance made this thesis possible. She has carried this work on through the days of difficulty when many of us would have let go… I have learnt a lot!

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Now this is finally done! For me the journey has been a huge rollercoaster with the ups and downs. Nevertheless, looking back at the time during this research I feel myself very lucky. Although it hasn’t always felt like this, it has been amazing times, spent in the lake, watching these seals that some people think as a myth. Again, I have been very fortunate to have so many people stand by me in all stages of the research. My warmest thanks to all my co-workers, especially the fellow PhD students from the team of “M’s”, including Anni, Miina, Mia and Sari. You have shared many of my good days and also quite many not so good days in this research and supported me in several ways, thank you for that! Warmest thanks are also due to Ursula and Raisa. I am most grateful for you all for the advice and encouragement. I thank also all the co-authors, especially Anu Valtonen for the great effort and guidance with the statistical analysis.

The field work of this thesis was carried out in Lake Haukivesi and the field staff stayed in Oravi camp “holvi”. I thank the Oravi village and all our project workers who were there and shared many moments (the best and worst) of this work with me. I would like to thank all of our students, especially Mirjami, Meeri and Riikka for the valuable help. Thanks to all the workers in field, especially Uippa, Ekku, Jani, Juhi and Vehmukka. Especial thanks are due to Terho Laitinen, our special field master, and his whole family for the dedication and support during these years. I thank also Ari Kirjavainen for the valuable help during the first years of my studies. I thank also the university technicians, especially Kari, Tuomo, Ilkka and Hanski and all the skilful staff who have helped me during these years. My appreciation goes also to Matti Savinainen, Kirsti Kyyrönen, Jorma Anttonen and Heikki Jeronen for technical support. I wish to thank Tuula Toivanen and Pirjo Marttinen for the skilful guidance and help with the bureaucratic things during these years. My warmest thanks go to Harri Kirjavainen for all the help and coffees during the project. My special thanks go to Juha Taskinen who assisted the research group in several ways and taught me a lot about Saimaa and the seals. It has been a privilege to work with you!

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Finally, I would like to express the warmest thanks to my family and relatives, mom and dad (+ Hugo, Ralla, Ruuti), Kaisa & Lauri (+ Etna, Hekla) and Miiko (+ Effi), the words are not enough to express the gratitude I feel for your loving support! I am so lucky to have you!

What next? Well, Life… ("just when I thought I was out, they pulled me back in…")

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, Niemi M, Kunnasranta M, Holopainen I J, Hyvärinen H. Vocal repertoire of the Saimaa ringed seal (*Phoca hispida saimensis*) during the breeding season. *Marine Mammal Science 25:920–930, 2009.*

II Niemi M, Auttila M, Viljanen M, Kunnasranta M. Home range, survival and dispersal of endangered Saimaa ringed seal pups: Implications for conservation. *Marine Mammal Science 29:1–13, 2013.*

III Niemi M, Auttila M, Viljanen M, Kunnasranta M. Movement data and their application for assessing the current distribution and conservation needs of the endangered Saimaa ringed seal. *Endangered Species Research 19:99–108, 2012.*

IV Niemi M, Auttila M, Valtonen A, Viljanen M, Kunnasranta M. Haulout patterns of Saimaa ringed seals and their response to boat traffic during the moulting season. *Endangered Species Research,* In press.

AUTHOR’S CONTRIBUTION

The original ideas for the articles were developed jointly by the authors. In the first article the present author was responsible for minor data collection and some analyses. Also, the present author was responsible together with the correspondent author for the writing of the manuscript in the case of article I and was mainly responsible for the methods, analyses and manuscript for articles II–IV. Several people (including the present author) participated in the data collection in each case.

Contents

1 Introduction

Ringed seals (*Phoca hispida*) are small-sized phocid seals living in icy waters, with a circumpolar Arctic distribution (Heide-Jørgensen & Lydersen, 1998). Their overall numbers amount to at least a few million (Reeves, 1998). The relic Fennoscandian populations were separated from the North Atlantic 8 000–9 000 years ago, to form populations of distinct subspecies in the Baltic Sea (*P. h. botnica)* and two freshwater lakes, Lake Ladoga (*P. h. ladogensis*) and Lake Saimaa (*P. h. saimensis*). Certain other ringed seal subspecies are also recognized in the marine environments outside Fennoscandian (see Amano et al., 2002; Berta & Churchill, 2012). Ice and snow play an important role in the life cycle of the ringed seals, as all the populations breed successfully only on ice, and a snowy habitat provides shelter during the breeding season (e.g. Smith & Stirling, 1975; Helle et al., 1984; Kelly & Quakenbush, 1990; Smith et al., 1991; Kelly, 2001; Kunnasranta et al., 2001; Härkönen et al., 2008; Kelly et al., 2010a; Jüssi, 2012).

1.1 THE RINGED SEAL IN LAKE SAIMAA

The Saimaa ringed seal is a geographically isolated and landlocked subspecies which has lived for over 8 000 years in the freshwater Lake Saimaa complex in south-eastern Finland (61º05′N, 27º15′E to 62º36′N, 30º00’E; Müller-Wille, 1969). It is the only mammal that is endemic to Finland. This small population differs from other subspecies genetically, ecologically and morphologically (Hyvärinen & Nieminen, 1990; Kunnasranta, 2001; Palo, 2003; Valtonen et al., 2012; Nyman et al., 2013).

1.1.1 Lake Saimaa as a habitat

As a habitat for the ringed seal, Lake Saimaa differs greatly from the environments of the other marine subspecies and also from that of the Lake Ladoga subspecies. Lake Saimaa is highly fragmented lake complex consisting of several interconnected water basins which are typically separated by narrow channels and sounds. It is some 4 400 km^2 in size but, although it is only about 190 km in length and maximum of 140 km in width, there are over 13 700 islands (Kuusisto, 1999). The total shoreline is ca. 15 000 km. On the other hand, the mean depth of the lake is only 12 m and the maximum depth 85 m. The lake is covered by ice for about five months per year, from the end of November to early May.

There is no other area in the world in which a whole seal population lives so close to humans as is the case in Lake Saimaa. The shores are inhabited by a human population of ca. 300 000, and the lake is used all the year round for recreation, fishing and transportation.

1.1.2 Conservation measures

The Saimaa ringed seal was hunted until its protection in 1955, and killing bounties were paid from 1882 to 1948 (Hyvärinen et al., 1999). The greatest threats to these seals since the protection order came into force have included environmental pollution, winter-time fluctuations in water levels, the destruction of suitable breeding sites, low demographic connectivity due to the small size of the population and by-catch through entanglement in fishing gear (Hyvärinen & Sipilä, 1984; Sipilä et al., 1990; Ranta et al., 1996; Kokko et al., 1998; Palo et al., 2003; Sipilä, 2003; Valtonen et al., 2012; 2013). The population size was lowest in the 1980s, with the smallest estimate of only 130 seals (Sipilä et al., 1990).

The current national legislative protection for the Saimaa ringed seal is to be found mainly under the Nature Conservation Act (1096/1996). In addition, the Act on the planning and construction of buildings (132/1999) aims to protect biodiversity and the nature environment by means of appropriate land use planning. Practical implementation of the conservation of the Saimaa ringed seal is under the Ministry of the Environment, and the conservation work is carried out by the Natural Heritage Services of Metsähallitus. The Saimaa ringed seal is also a focus of legislative protection under the European Commission's Habitats Directive (Council Directive 92/43/EEC) and is included among the annex IV species. According to this directive and under national law, all actions that disturb the Saimaa ringed seals, impair their breeding or destroy their breeding and resting sites are prohibited. The Finnish National Shoreline Conservation Programme, established in 1990, and the European Natura 2000 ecological network both protect the breeding habitats of the Saimaa ringed seal (Sipilä, 2003). In addition, the Directive maintains that accidental deaths should not be allowed to have a significant negative impact on the endangered population.

By-catch, especially due to recreational and subsistence gill net fishing, has been and still is the largest threat to the Saimaa ringed seal. This has been the case since the 1960s, when nylon replaced cotton as material from which the fishing gear was made (Hyvärinen et al., 1999). Unlike the situation in many other countries, gill nets are commonly used in recreational and subsistence fishing in Finland as well as in commercial fishing (Salmi et al., 2000). Furthermore, the inland waters are owned mostly by local people and the state, in association with land holdings (Salmi & Muje, 2001; Salmi, 2012). The first voluntary-based ban on the use of gill nets during the most critical period for pup survival (from 15 April to 30 June) was established in 1982 in an area covering 1.5% of the total surface area of Lake Saimaa (Sipilä, 2003). This spring-time fishing restriction remained voluntary until April 2011, when it was incorporated into a government decree (294/2011) based on the Fishing Act (286/1982) in order to further improve the conservation status of the Saimaa ringed seal population. The restriction area has also been extended in the course of time, mostly during recent years, so that in 2012 it covered over 45% of the surface area of the lake (based on a map produced by South Savo ELY Centre, 2012).

Spatially the restriction consists of the decree area and areas based on voluntary contracts. Financial compensation is paid to the owners of the water for signing the voluntary contract. In addition to the spring-time fishing restrictions, the types of fishing gear regarded as the most dangerous for seals (e.g. fish traps with an opening larger than 150 mm, strong-mesh gill nets, salmon traps, hooks baited with fish, multifilament nets and trammel nets) have been forbidden by year-round government decree (295/2011) since 1999, in an area that covers ca. 40% of the lake (based on a map produced by Metsähallitus, 2012).

There are over 60 000 summer cottages on the shores of Lake Saimaa, and the number is increasing (Ministry of the Environment, 2011), as also is shipping and passenger traffic via the Saimaa Canal (Pienimäki & Leppäkoski, 2004). The growing number of cottages on the shoreline in particular is regarded as a potential threat to the Saimaa ringed seal (Sipilä, 2003). In practice, the land use planning limits the number of new buildings close to the shoreline in the Saimaa ringed seal breeding areas (Wilson et al., 2001; Sipilä, 2003; Ministry of the Environment, 2011).

Changes in water level have occasionally caused the ice cover to break up and damaged the seals' lairs during the winter time, causing an increase in the proportion of stillborns (Sipilä, 2003). Consequently, the Saimaa ringed seal was also taken into account in the 1991 act governing regulation of the outflow from Lake Saimaa (1331/1991), the aim being to stabilize the fluctuations in the water level from the beginning of the ice cover season until 20 March within a 20 cm range (Ministry of the Environment, 2011).

Due to the various conservation measures, the ringed seal population of Lake Saimaa has finally increased from the low numbers recorded in the mid-1980s' – mostly during the last decade. Today, the population comprises around 300 animals (Metsähallitus, 2012). At the same time, however, the first signs of the effects of climate change have been observed, in that newborn pups have been found on the ice in spring without the protection of lairs due to the mild winter. Without the shelter of the snow lair, nursing may be disturbed. This may lead to high pup mortality, either directly or via low pup weight at weaning, which increases the risk of by-catch mortality (Sipilä, 2003). In addition, the lair provides shelter against low temperatures and predators (e.g. Smith & Stirling, 1975), and the loss of this protection may be fatal. Thus increasingly early snow melts and shortages of snow may have negative long-term consequences for ringed seal pup survival (Kelly et al., 2010b).

Mainly due to the threats posed by by-catch, the fragmented population structure and climate change, the Saimaa ringed seal is categorized as a critically endangered both nationally and internationally (Rassi et al., 2010; Kovacs et al., 2012). This implies that the population faces an extremely high risk of extinction in the wild (IUCN, 2001). The first milestone in Saimaa ringed seal conservation will be to reach a population of 400 seals by 2025 (Ministry of the Environment, 2011). The long term goal is to attain a favourable conservation status: a population can maintain itself at a viable level, its natural range is not likely to be reduced in the foreseeable future and the habitat will be sufficiently large to maintain such a population on a long-term basis (Jones, 2002).

1.2 ANIMAL BEHAVIOUR AND CONSERVATION

The main objectives of conservation biology are identifying populations that are at risk, studying the causes of their decline, attempting to mitigate of those causes and assessing the effectiveness of the mitigation measures (Read, 2010). As for conservation behaviour, the aim is to apply the knowledge on animal behaviour into practice in order to solve wildlife conservation problems (e.g. Blumstein & Fernández-Juricic, 2004; Blumstein & Fernández-Juricic, 2010). The behavioural aspect should always be taken into consideration by wildlife managers (Festa-Bianchet, 2003).

1.2.1 Vocalization

The purpose of vocalization in marine mammals is communication between individuals or locating targets by echolocation (Berta et al., 2006). Pinnipeds are amphibious animals that use their hearing both in air and under water (Kastak & Schusterman, 1998; Au & Hastings, 2008). They have better low-frequency hearing in air than do most terrestrial mammals (Berta et al., 2006) and they are more sensitive to high frequencies under water (see review by Au & Hastings, 2008).

Phocid seal calls have been associated with mating, mother-pup interactions and territoriality (Richardson et al., 1995). Airborne sounds are assumed to be connected with social functions such as the threat calls of territorial breeding males, or the pup-attraction calls of mothers (Richardson et al., 1995; Berta et al., 2006; Van Opzeeland et al., 2008). Most species have specific vocalizations that mother-pup pairs employ for recognizing and locating each other (Berta et al., 2006). Variety of underwater vocalization is also often related to breeding activities (Richardson et al., 1995) such as attracting female partners (Hanggi & Schusterman, 1994), and/or male-male competition (Hanggi & Schusterman, 1994; Hayes, 2002), advertising sexual readiness among mature females (Rogers et al., 1996), and territorial declaration (Thomas & Kuechle, 1982; Thomas & Stirling, 1983). Geographical variation between individual repertoires has also been recognized (Thomas & Stirling, 1983; Van Parijs et al., 2003). Although underwater clicks have been recorded from pinnipeds (e.g. Møhl et al., 1975; Hyvärinen, 1989; Kunnasranta et al., 1996), there is no evidence to confirm their use for echolocation (Schusterman et al., 2000).

The hearing of the ringed seal is semi-adapted to underwater conditions (Richardson et al., 1995), with best heard frequencies underwater of 2-50 kHz (Au and Hastings, 2008) and a maximum frequency of 90 kHz (Terhune & Ronald, 1975). They are known to produce four types of sound: barks, growls, clicks and yelps, with dominant frequencies of under 5 kHz (Stirling, 1973; Cummings et al., 1984). These calls are often faint and the range is assumed to be low, less than 1 km (Stirling et al., 1983;

Cummings et al., 1984). The number of calls increases during the breeding season (Stirling, 1973; Stirling et al., 1983; Cummings et al., 1984). Ladoga ringed seals are known to produce at least six types of underwater sound, with dominant frequencies in the range 0.2–4 kHz: clicks, burst pulses, knocking, chirps, yelps and growls (Kunnasranta et al., 1996; Kunnasranta, 2001), of which the burst pulses and knocking sounds have not been described earlier in ringed seals (Kunnasranta et al., 1996). In addition, they are known to produce eight types of sound in air when hauled out in herds (Sipilä et al., 1996). The underwater vocalization is connected with social behaviour of the ringed seals (Stirling, 1973; Kunnasranta et al., 1996). The solitary Saimaa ringed seals are known to produce clicks in the 0–20 kHz range (Hyvärinen, 1989) and yelps made by pups (Kunnasranta, 2001).

1.2.2 Home range, dispersal, and site fidelity

The implementation of appropriate protection measures for endangered species requires knowledge of their fine-scale movement behaviour (Schofield et al., 2009). For example, as by-catch is a severe threat to many marine mammal species and populations (Lewison et al., 2004; Read, 2008; Reeves et al., 2013), a knowledge of the movement patterns of individuals is needed in order to assess by-catch (Reeves et al., 2013). The most reliable techniques for determining the spatial ecology of free-ranging animals are remote monitoring using various telemetry techniques, such as logging and relaying of data on movements, behaviour and environment (Cooke, 2008; Rutz & Hays, 2009).

The motives behind of movement patterns in marine mammals include feeding, breeding, giving birth, lactation, moulting and for pinnipeds also haul out (Stern, 2009). Ringed seals haul out either on the ice or on terrestrial sites (Smith, 1973; Finley, 1979; Kingsley & Stirling, 1991; Hyvärinen et al., 1995; Heide-Jørgensen & Lydersen, 1998; Kunnasranta, 2001; Kunnasranta et al., 2002; Härkönen et al., 2008; Freitas et al., 2008; Kelly et al., 2010a). In addition to moulting and resting, the reasons for haul out may include the reduction of thermal stress, and possibly also underwater predator avoidance in marine environments (Freitas et al., 2008).

Dispersal is certainly one form of movement, although there are many definitions for it. The traditional definition is movement by an individual from its place of birth to the place where it reproduces (Howard, 1960), but dispersal may also be movement between breeding sites (Kenward et al., 2002). Dispersal may be voluntary or forced (e.g. by adult aggression; Howard, 1960), and the decision on whether or not to disperse depends on species, gender, or population-specific behaviour patterns (Woodroffe, 2003). Among mammals it is the males that are normally the main dispersers (Greenwood, 1980), but also several factors that affect the dispersal decision can be identified, most notably genetic factors, habitat quality, social pressure and individual experience (Kenward et al., 2001b). The detection of dispersal may be complex, and subjective rules have often been used for its determination (Kenward et al., 2002).

An animal's home range is traditionally defined as the area that it uses in its normal activities of foraging, mating and caring for its young (Burt, 1943), but it may also be described as the area that it repeatedly traverses in the course of its life (Kenward, 2001). As an animal excurses into new areas, its home range expands, so that it may be necessary to set a time frame for home range determination if an animal moves about on a seasonal basis (Kenward et al., 2002; White & Garrott, 1990). Although unidirectional dispersal, migratory movements and sporadic movements are not traditionally included in a home range, repeated traverses such as there-and-back movements may be made within a home range (Kenward, 2001; Kenward et al., 2002). Overall, there are numerous methods to choose from for estimating home range and core area boundaries, and which is the best estimator is dependent on the sample size, how the animals are moving and the biological issue to be resolved (Kenward et al., 2001a).

Site fidelity is a tendency to return to a previously occupied location (Switzer, 1993). Seals are longevous species which typically exhibit high fidelity to their breeding sites (Boyd, 2002). Dispersal is not always an on-off process and the decision as to whether to disperse may be tied in with the ecology of the individuals concerned. Grey seals (*Halichoerus grypus*), for example, show a high degree of fidelity to their breeding sites, but as the population increases, they move to new areas to breed (Pomeroy et al., 2000a). While adult seals show a high degree of breeding site fidelity and it is mostly the juveniles that disperse, a disturbance or breeding failure can lead to emigration of all the age and sex groups in a population (Boyd, 2002). In addition to breeding site fidelity, phocid seals also seem to show some degree of philopatry, i.e. returning to breed at the site where they were born (Stanley et al., 1996; Pomeroy et al., 2000b). However, while ringed seals have been shown to exhibit strong inter-annual site fidelity with respect to their breeding sites (Helle et al., 1984; Sipilä, 1990; Kelly et al., 2010a), the theories regarding philopatry vary. Davis et al. (2008) found a lack of population structure in the Arctic, which would suggest no philopatry, but many of their samples were collected outside the breeding season, which may have skewed the results (Kelly, 2009; Kelly et al., 2009). A certain degree of philopatry has been found among females in Lake Saimaa, (Valtonen et al., 2012).

1.3 AIMS OF THE STUDY

The specific aims of this thesis were to provide new and urgently needed information on the behaviour of free-ranging Saimaa ringed seals and implications for conservation, especially in order to mitigate by-catch and human induced-disturbance. The more detailed aims were:

1. to study the breeding and nursing time behaviour of the Saimaa ringed seal (I & II).
2. to determine the movements and dispersal patterns of pups before and after weaning (I, II & III).
3. to describe the haulout behaviour and movement patterns of adult seals (III & IV), and
4. to provide information for use in conservation, especially when mitigating anthropogenic disturbance, planning sustainable land use close to the shoreline, imposing spring-time fishing restrictions, and drawing up year-round regulations concerning the banning of the fishing methods that pose the greatest danger to seals (I, II, III & IV).

2 Material and methods

2.1 STUDY AREA

The research was carried out in the Lake Haukivesi and Lake Joutenvesi basins (62°09′N, 28°18′E) of central Lake Saimaa (Fig. 1). Both basins are typical of this part of the lake system, with relatively shallow water (average depth 9 m, maximum 55 m) and a large number of islands and islets. There are 65 Saimaa ringed seals in the Haukivesi basin, with approximately 15 pups born annually, and 23 seals in the Joutenvesi basin, with 3 pups born annually (Metsähallitus, 2012). One of the two National Parks in Lake Saimaa is situated in Lake Haukivesi (Fig. 1) and this is a popular tourist destination offering a variety of outdoor activities (Metsähallitus, 2013).

2.2 VOCALIZATION STUDIES

The vocalization study was conducted during the spring in 1999 and 2002–2008 (I). Six Saimaa ringed seal mother-pup pairs (with the pup approximately 1-2 months of age) were studied in the vicinity of the birth lairs in April 1999 and 2002–2006 (I, Table 1) using in-air and underwater sound recordings and video monitoring. The recordings were mainly made from dawn to dusk with some round-the-clock monitoring at a distance of 5–20 m from the vocalizing pup, while the distance from the vocalizing mother underwater was often unknown. Water depths at the recording locations ranged from 1 to 5 m.

Additional underwater vocalization recordings of unidentified Saimaa ringed seals were made in March 2007 and 2008, during the early part of the breeding season. At least one VHF-tagged adult male and two adult females with pups were known to be present in the recording area in 2007, and similarly one VHF-tagged adult female and one adult male in 2008. The underwater recordings were made approximately 400–600 m away from the nearest islands with known birth lairs.

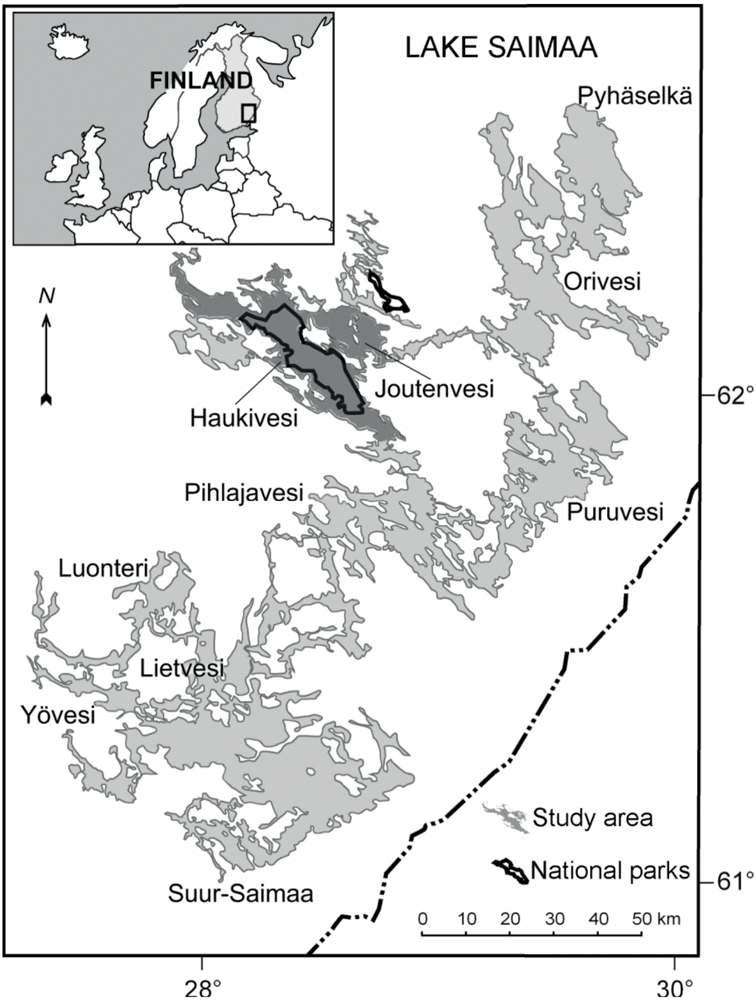


Figure 1. *Map of Lake Saimaa.*

The airborne vocalizations were recorded using a stereo tape-recorder with a directional microphone, and the underwater vocalizations with minidisk and digital audiotape recorders with an omnidirectional wideband probe hydrophone. In addition, a video camera was used to record vocalizations and monitor the behaviour of the mother-pup pairs when they were basking on the ice. The underwater behaviour of the seals was monitored using underwater digital video cameras connected by a 50 m cable to a video processor and monitor (recording video camera). The vocalization parameters were analysed from spectrograms using Raven 1.2 software for Macintosh.

Table 1. *Details of the Saimaa ringed seals studied. (-) = no data, F = female, M = male, hydro = hydrophone, micro = microphone, VHF = radiotransmitter, GPS = GPS-phone tag.*

ID	Sex	Age class	Method	Tracking period	Mass (kg)	Article
-	F	mother	micro	18.04.99	-	I
pup1	-	& pup			-	
-	F	mother	hydro	12.04.02–24.04.02	-	I
pup2	-	& pup			-	
-	F	mother	hydro	11.04.03–24.04.03	-	I
pup3	-	& pup			-	
F4	F	mother	hydro	04.04.04–23.04.04	-	I
pup4 (OI10)	M	& pup			-	
-	F	mother	hydro	07.04.05–16.04.05	-	I
pup5	-	& pup			-	
F6	F	mother	hydro	14.04.06–27.04.06	-	I
pup6	-	& pup			-	
adult1	-	adult	hydro	05.03.07–06.03.07	-	I
adult2	-	adult	hydro	05.03.08–06.03.08	-	I
RA10*	M	pup	VHF	02.05.10–31.05.10	27	II
RU95	F	pup	VHF	04.05.95–13.07.95	24	II, III
ER07	F	pup	VHF	25.04.07–08.11.07	18	II, III
MA07*	M	pup	VHF	24.04.07–26.05.07	18	II, III
OT08*	M	pup	VHF	17.04.08–24.05.08	31	II, III
TE08	F	pup	VHF	26.04.08–23.12.08	26	II, III
AL08	F	pup	VHF	23.04.08–22.10.08	28	II, III
TJ09	M	pup	VHF	12.04.09–31.05.09	17	II, III
YL10*	M	pup	VHF	06.05.10–26.07.10	26	II, III
VA10	F	pup	VHF	01.05.10–02.07.10	18	II, III
LI11	F	pup	VHF	14.04.11–08.06.11	25	III
AL11	M	pup	VHF	05.05.11–04.01.12	18	III
OI10	M	adult	GPS	27.05.10–28.05.10	57	III
TA10	M	adult	GPS	12.12.10–26.12.10	65	III
HE07	F	adult	GPS	01.06.07–09.12.07	57	III,IV
KJ07	M	adult	GPS	25.05.07–29.12.07	52	III,IV
TO07	M	adult	GPS	03.06.09–28.03.10	55	III,IV
VI09	M	adult	GPS	26.05.09–11.12.09	124	III,IV
OL10	F	adult	GPS	31.05.10–02.04.11	59	III, IV
LI10	F	adult	GPS	21.05.10–15.07.10	48	III, IV
ER11	M	adult	GPS	20.05.11–22.09.11	66	III, IV
TE07	F	adult	GPS	31.05.11–13.02.12	52	IV

**entangled in fishing gear*

2.3 TELEMETRY STUDIES

The VHF radiotelemetry study of Saimaa ringed seal pups (II, III) was conducted during the years 1995 and 2007–2011. Altogether 12 pups, each about two months old, were provided with VHF radio tags (Table 1, Fig. 2a), and tracked once a day 2-7 times per week. The GPS-telemetry study of 10 adults was conducted during the years 2007–2012 (III, IV; Table 1, Fig. 2b) for the collection of data on their locations, water temperature, time, haul-out and dives. The data were downloaded via the GSM network. The GSM range is highly comprehensive in the Saimaa area and presents no difficulties for downloading. The location interval (fastloc/fastcat) in this study was 20–30 min and the GPS call interval 12 h.

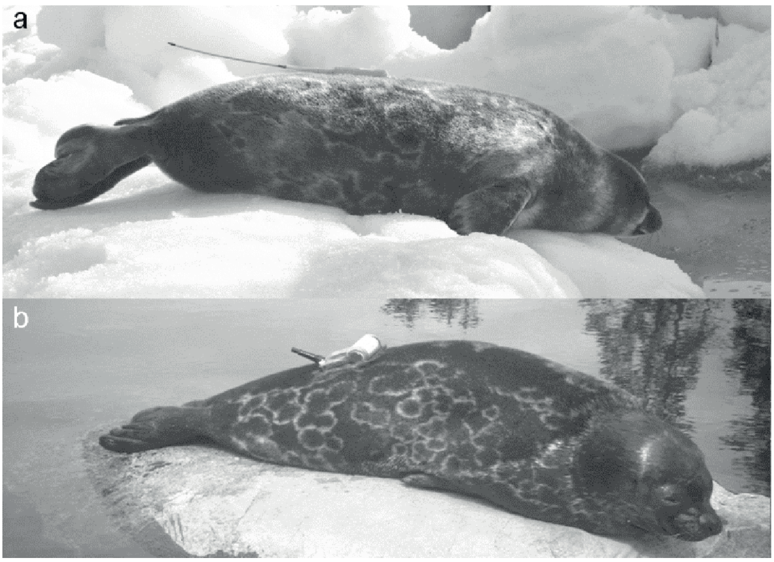


Figure 2. *Saimaa ringed seal a) pup with VHF radio tag attached to the dorsal pelage, and b) adult with GPS phone tag attached to the dorsal pelage.*

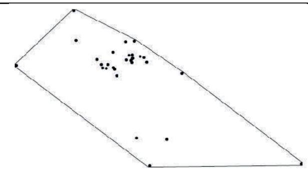
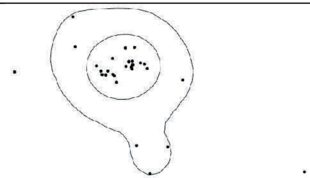
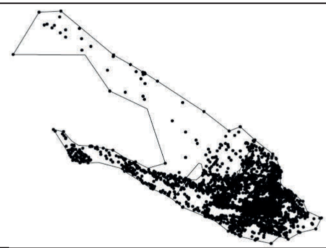
The pups were captured from the water in the vicinity of their nursing sites using gill nets of mesh size 60–80 mm, or with a modified dip net while they were basking on the ice. All the pups were tagged near the end of the nursing period after they had shed their lanugo hair. The adult seals were captured from their haul-out sites during the moulting season in early summer using modified tangle nets (bar length 150 mm). All the seals were restrained manually while a tag was attached to the dorsal post-moult pelage with two-component epoxy glue (Fig. 2). For later identification, a uniquely numbered plastic roto tag was attached to the hind flipper of each seal. The tagged animals were released in the vicinity of their capture site.

The methods chosen for describing the movements, home ranges, areas of intensive usage (home range core areas) and survival of the pups, were 100% minimum convex polygon (MCP 100%) and 95% & 50% fixed kernel contours (II, III, Table 2). In addition, the *a*-LoCoH 100% & 50% method were used to describe the movements, home ranges and areas of intensive usage (home range core areas) of the adult seals (III, IV, Table 2). Further, nursing sites, breeding areas and current distribution areas were assessed on the basis of the lair census data (©database maintained by Metsähallitus, 2012) and the average home ranges (MCP 100% and *a*-LoCoH 100%) and compared with the coverage of the fishing restrictions (II, III).

The haulout data provided by the GPS tags were used to calculate the general haulout patterns of the adult seals and to describe the characteristics of their haulout sites during the open-water season (between the break-up of the ice in spring and freezing over in autumn, normally from early May to late November) in 2007–2011 (IV, Table 1). In addition, responses of unidentified seals to outboard motor boats (categorized as no response, alert or entered the water) were recorded at the haulout sites during the moulting seasons in the springs of 2006–2010 (IV).

The home ranges of the pups were analysed using the Ranges8 software and Hawth's tool extension (Beyer, 2004) in ArcGIS 9.3 (II, III). The home ranges of the adults were analysed using the 'adehabitat' package (Calenge, 2006) for the R statistical software (III, IV). All the distance measurements were made using Hawth's tool extension in ArcGIS 9.3 (III, IV). Further, statistical analyses were conducted using SPSS Statistics 19 (IV).

Table 2. *Home range estimators used to study the spatial ecology of the Saimaa ringed seal.*

Home range estimator	**Description**	**Example**	**Pros and cons**	**Article**
Minimum convex polygon, MCP	Draws a line round the outermost location points to a form of a convex polygon (White & Garrot, 1990).		+ easiest and still the most widely used method + suitable for conservation purposes - easily overestimates the home range area - does not take the density of the locations into account	II, III
Fixed kernel (kernel density estimator), FK	Calculates the probability of finding an individual in a particular location using non-parametric statistics (Worton, 1989).		+ suitable for VHF data + shows the areas where the animal might be although not observed + performs well in the core areas - important areas such as travel corridors may be left out of the home range, so that the method is not suitable for conservation purposes (lack of a 100% distribution) - sensitive to a smoothing factor	II
Adaptive Local convex hull, *a*-LoCoH	A non-parametric kernel method that is based on local nearest neighbour convex hulls, generalizes the MCP method (Getz et al., 2007).		+ takes boundaries (such as islands) as determined by geographical or physiographic features into consideration + suits well for large datasets + suitable for conservation purposes - does not fit for small datasets such as in the present VHF study	III, IV

2.4 ETHICS OF THE STUDY

The safety of the seals and researchers has been considered as a first priority. The research group had the skills required for handling the seals and the responsible personnel were competent to conduct animal experiments. As the Saimaa ringed seal is protected by very strict national legislation, the research needed to be well justified. It was therefore carefully pre-evaluated and was conducted under 15 permits obtained from the local environmental authorities (most recently ESA-2008-L-519-254 & MH5648/662/2010) and the Animal Experiment Board in Finland (recently ESAVI-2010-08380/Ym-23).

The general criteria for the treatment of animals (Gales et al., 2009; 2010) were complied with as strictly as possible without compromising the aims of the research. The maximum number of animals to be studied per year was laid down in the permits. Existing data from previous studies of the Saimaa ringed seal were used whenever possible. Information on the behaviour of other seal species could not be used in any comprehensive manner because Lake Saimaa differs from all the other environments in which ringed seals live. The potential negative effects of the research were minimized by using the smallest possible instruments designed for aquatic mammals while still gaining the maximal amount of information. The tags concerned in this study are widely used in marine mammal research and weighed less than 1% of the animal's total weight. The recommendation is to use tags that are less than 3–5% of the animal's body mass, or smaller percentages in the case of birds and aquatic animals (Kenward, 2001; see also Cuthill, 1991). The capturing methods were designed to entail the smallest risk possible, the nets were supervised and the animals were released from the net immediately and restrained manually. Individual differences among the seals were taken into consideration, e.g. by obscuring an animal's vision only if it stayed calmer that way. Heat stress was minimized by monitoring the temperature of the hind flippers. The tags were fixed to the fur using thin layers of glue to minimize heating (Field et al., 2012). The average duration of tracking was ca. 6 months, with a maximum of 10 months. Furthermore, the research was conducted with paying attention to its impacts on the environment, minimizing the potential disturbance to the flora and fauna of the area, including nesting birds.

3 Results and discussion

3.1 BEHAVIOURAL ECOLOGY OF THE SAIMAA RINGED SEAL

This is the first time that the behavioural ecology of Saimaa ringed seal pups has been studied. It is known that these seals give birth to a single pup in mid-February to mid-March in snow lairs which are normally situated on the shores of small islands (Helle et al., 1984; Sipilä, 1990). The present results suggest that the natal sites are actively used by the pup and mother until late spring, even after the sheltering snow lair has melted (I). At the same time the mother and pup are vocally active, with a repertoire of vocalizations that is much broader than has previously been thought (Hyvärinen, 1989; Kunnasranta, 2001). In addition to mother-pup vocalizations, Saimaa ringed seals also produced rapid bursts of knocks in March (I, Table 3). As mating is assumed to take place during the nursing period in March after parturition (Sipilä & Hyvärinen, 1998), these rapid bursts of knocks are assumed to be related to the species' breeding behaviour. These adult calls were more rapid than the calls of the mother recorded from the mother-pup pairs later on during the nursing season in April. The slower series of knocking sounds generated by the mothers were similar to with the knocking calls of Ladoga ringed seals (Kunnasranta et al., 1996), although some differed from the latter by including a growl (I, Table 3). Similar knock-like vocalizations have also been described in the spotted seal (*Phoca largha*; Beier & Wartzok, 1979), walrus (*Odobenus rosmarus rosmarus;* e.g. Stirling et al., 1987; Sjare et al., 2003), grey seal (Asselin et al., 1993), Weddell seal (*Leptonychotes weddelli;* Thomas & Kuechle, 1982) and harp seal (*Pagophilus groenlandicus;* Møhl et al., 1975), but not in ringed seals in marine environments. Cummings et al. (1984) nevertheless mentioned a knocking sound produced by ringed seal in the Kotzebue

Sound, Alaska, but as it was found only infrequently, no further description of it was provided.

Table 3. Description of vocalizations produced by Saimaa ringed seals (Article I).

	Elements	Duration (ms)
adult	knocks (mean n of knocks = 33)	1 258
mother	knocks (mean n of knocks = 5)	672
	knocks with a growl	1 160
pup	harmonic, subharmonic, chaos and frequency jumps	853

The pups vocalized both in air and under the water by means of calls of a harmonic structure with non-linear dynamics (I, Table 3), similar to the calls of pups of the grey seal (Mc Culloch et al., 1999), harp seal (Van Opzeeland & Van Parijs, 2004), Weddell seal (Collins et al., 2006) and harbour seal (Khan et al., 2006).

The average size of a pup's home range during the nursing season was ca. 2 km^2 (II, III, Table 4), which is similar to that of an adult ringed seal in a marine environment during the subnivean period (Kelly et al., 2010a). The pups dispersed from their natal sites in mid-May (II). It has been assumed that the nursing period in Saimaa lasts 7–9 weeks (Sipilä & Hyvärinen, 1998), which is the longest among phocid seals (Riedman, 1990). However, the average time of dispersal of the pups studied here suggests an even longer nursing period (ca. 9–12 weeks). This is supported by the known birth date of one pup, which was nursed for around 10 weeks. It is known that foraging is learned prior to weaning and that the submerged behaviour of ringed seals is relatively well-developed at a young age (Lydersen & Hammill, 1993). After weaning, the movements of the pups were random and they were capable of moving long distances on a scale of Lake Saimaa. Maximum movements between consecutive locations were in the range of 3–15 km. In addition, the distances from the pups' natal sites to their furthest locations were in the range of 3–25 km by the end of June. The pups were exploring their habitat and did not seem to settle during the study period. Dispersal was defined here as the time when the pup left its natal site to explore other habitats. As the study spanned less than a year, however, no information is available on movements between the age of one year and maturity. Genetic research indicates that at least the females are philopatric (Valtonen et al., 2012).

Table 4. Summary of the home ranges of Saimaa ringed seals (Articles II & III).

	Method	Mean **home range** ± SD (km^2)	Range (km^2)	Seals tracked (n)	Article
Pups					
nursing[a]	100% MCP	**1.97** ± 2.4	0.08–6	7	III
spring time fishing restriction[b]	100% MCP	**68.1** ± 65	3–162	6	II
total[c]	100% MCP	**93.9** ± 69	3–188	7	III
core area[b]	50% FK	**18.3** ± 19		6	II
Adults					
total[d]	100% LoCoH	**92.3** ± 54	20–172	7	III
core area[d]	50% LoCoH	**4.59** ± 3.7	0.5–11	7	

a from tagging (Table 1) to a week after the last sighting of the mother-pup pair, mean 24 days
b from tagging (Table 1) to the end of June, mean 62 days
c from tagging (Table 1) to the telemetry tag dropping off, mean 154 days
d from tagging (Table 1) to the telemetry tag dropping off, mean 199 days

The moulting of seals older than one-year takes place in the late spring, May–June, after the ice has melted (Hyvärinen et al., 1995; Kunnasranta, 2001; Kunnasranta et al., 2002). At the time, 62% of the Saimaa ringed seals that were approached responded to the outboard motor boat mostly by lifting their head or moving their body (being alert) when the boat was at median distance of 240 m away (range 30–600 m; IV). It is normal, however, for hauled out ringed seals to show vigilance by lifting their heads every 0.5–1 min for a few seconds to scan their surroundings (Stirling, 1974). Overall, prey animals tend to show more vigilance when the perceived risk of predation is high (Frid & Dill, 2002). However, moulting seals are more reluctant to enter the water (Moulton et al., 2002). The median distance at which the boat induced no response among the moulting Saimaa ringed seals was 300 m (range 50–600 m), but when the boat approached closer, to around 150 m (range 30–500 m), the seals entered the water (IV).

It is predicted that a fast, direct approach and larger size disturbance stimulus or larger group of such stimuli, as also a greater distance from shelter and a low cost of fleeing, will increase the probability of fleeing (Frid & Dill, 2002). Disturbance has even been shown to lead to emigration in the case of grey seals (Boyd, 2002). Most of the present approaches (87%) were made towards a solitary seal (IV). It has been shown that a single ringed seal is as effective as a group of seals in examining its surroundings for potential threats (Stirling, 1974; Smith & Hammill, 1981). On the other hand, the fact that Ladoga ringed seals haul out in herds has been explained by a higher probability of detecting possible dangers (Agafonova et al., 2007).

Table 5. *Summary of the haul-out behaviour of the Saimaa ringed seals during the open-water season (Article IV).*

	Average ± SD	**Max**
Haulout duration (h)	6.0 ± 4.6	26.4
Time between the successive haulout events (h)	26.2 ± 29.3	434.6
Haulout sites / individual (n)	13.0 ± 4.6	21
Distance between the haulout sites (km)	2.5 median ± 4.6	22.7
Intensively used haulout sites / individual (n)	6.6 ± 2.1	10

During the post-moult period Saimaa ringed seals rest in terrestrial sites on the rocks on shorelines, mainly nocturnally (Hyvärinen et al., 1995; Koskela et al., 2002; Kunnasranta et al., 2002; IV), as is also the case with Baltic ringed seals (Härkönen et al., 2008). About 20% of a Saimaa ringed seals total time is spent hauled out (Hyvärinen et al., 1995; Kunnasranta, 2001; IV), with this activity declining towards the autumn, as in the Arctic (Teilmann et al., 1999; Kelly et al., 2010a). Post-moult haulout events among Saimaa ringed seals during the open-water season (ca. 6 h, IV, Table 5) are twice as long as those reported for Arctic ringed seals in autumn (Teilmann et al., 1999; Born et al., 2002). Saimaa ringed seals had an average of 13 haulout sites each during the open-water season (IV, Table 5). These sites of an individual seal were situated an average of only 2.5 km apart.

About a half of the sites were used intensively and they were mostly situated on the eastern and southern shores of small islands less than 5 ha in size on average (IV).

Saimaa ringed seals used both shallow and deep water areas in their home ranges (II, III), perhaps because they were foraging mainly on small, schooling fish in both pelagic and littoral areas (Kunnasranta et al., 1999; Auttila et al., 2013). The adult seals had total (100%) home ranges that were similar in size to those of the pups (III, Table 4). However, it should be remembered that different methods were used for tracking the pups (VHF) and the adults (GPS) and that the VHF method may miss significant animal movements, so that the home range estimate may be smaller than the corresponding GPS estimate (Kochanny et al., 2009). Furthermore, the movement patterns were different; the adult seals had stabilized their home ranges, but they made sporadic movements or had different home ranges during the open-water and ice-covered seasons, which increased their total home ranges. Similar movement patterns with sporadic movements by some adults have also been found in Arctic ringed seals (Gjertz et al., 2000; Kelly et al., 2010a). Although only some adults moved to different areas in autumn in Saimaa, ringed seals of all age groups have been found to migrate in Canada’s Western Arctic in autumn, prior to the freezing of the sea (Harwood et al., 2012).

The pups’ home ranges did not stabilize during the study period. They moved more than the adults, as could be seen from the larger core areas (18 km^2) of their home ranges compared with those of the adults (4.6 km^2; Table 4). Juvenile seals of various species, including the ringed seal, are known to wander (Stewart et al., 1996; Ridoux et al., 1998; Lowry et al., 2001; Freitas et al., 2008; Crawford et al., 2012), in addition to which there may be differences in timing and habitat choice between adults and immature seals (Burns et al., 1999; Bornemann et al., 2000; Krafft et al., 2007; Crawford et al., 2012). In many cases inexperienced juveniles exhibit exploratory movements and are more active than adults (Lamberty & Grower, 1991; Sjöberg & Ball, 2000).

3.2 IMPLICATIONS FOR CONSERVATION

The sedentary lifestyle with sporadic movements, together with individual differences in behaviour patterns, makes the conservation of the Saimaa ringed seal highly demanding. Vocalization may be more important factor in the mating tactics of the Saimaa ringed seal than has been earlier assumed, as the rapid bursts of knocks were only apparent during the early breeding season in an area known to be inhabited by adult seals (I). The exact timing of parturition remains unknown in many cases, although, one female, tracked in 2007, was known to give birth around 12 March. Taking these factors into account, the time frame (from freezing over until 20 March) set for the avoidance of water-lever fluctuation during the ice-cover season in order to prevent harmful impacts may be too short. Instead, stabilizing the fluctuation up to the end of the ice-cover season should be considered to prevent early destruction of the lairs.

The natal site is important for a pup until it disperses, in mid-May on average (I, II). During the nursing season and up to the time of dispersal, the pup moves about in a small area near its nursing site (Table 4), which highlights the need to conserve such sites (Table 6, Fig. 3, II). These sites include an 800 m buffer zone around each observed birth lair, based on the average home range of the pre-weaned pups (III), which should be taken into consideration when planning conservation measures. Furthermore, in order to mitigate the long-term sources of disturbance by means of sustainable land use planning in particular, the haulout areas of Saimaa ringed seals should also be identified and conserved throughout the species' distribution area in addition to the nursing sites. Some characteristics can be found to describe the most typical haulout sites, as the present research showed that they were mainly situated on the rocks on the eastern and southern shores of small islands (< 5 ha in size; IV). One should bear in mind that during the winter, when there is enough snow piled up into drifts on the shores of the islands, the seals dig a lair in the snow over their breathing holes (Sipilä, 1990). These subnivean lairs, which are used for both haul out and breeding, are typically situated on the northern or eastern shores of islands (Helle et al., 1984; Sipilä, 1990).

Table 6. *Glossary of terms used to describe the time and closure areas and the parameters used to direct the Saimaa ringed seal conservation decisions considered in this study (Article III).*

Term	**Description**	**Current area / proportion of the lake size**
Potential distribution area	Lake Saimaa	4 400 km^2 / 100%
Current distribution area	Based on seal movement data and lair locations in the 2000s.	3 100 km^2 / 70%
Current breeding area	Based on pups movement data and birth lair locations in the 2000s.	2 240 km^2 / 51%
Nursing sites	Separate areas around each birth lair found in the 2000s based on movement data for pups prior to weaning. N = 450 sites altogether.	2 km^2 per nursing site / 0.05% per site
Spring-time fishing restriction	Gill net fishing is banned in the seals' breeding area from 15 April to 30 June.	2 000 km^{2a} / 45%
Gear type restriction	Using certain types of fishing gears[b] is banned in the main distribution area of the Saimaa ringed seal all the year round.	1 740 km^{2c} / 40%

a Of which the decree applies to an area of ca. 1850 km^2. Situation on 16 April 2012; © data from South Savo ELY Centre, 2012
b E.g. specified fish traps, hooks baited with fish, strong-mesh gillnets, multifilament nets and trammel nets
c ©database maintained by Metsähallitus, 2011

Recently, the home ranges of the pups (II) have been taken into consideration when planning the spatial coverage of the spring-time fishing restrictions (government decree, 294/2011), and existing data on pup movements is employed annually when new areas are to be suggested for inclusion under the restriction. In 2012 the spring-time fishing restrictions covered 83% of the current breeding area of the Saimaa ringed seal (Table 6). Altogether 5 of the pups studied here (total N = 12 plus N = 2 in an additional study in 2012) were caught in fishing gear. The temporal coverage of the spring-time fishing restriction may be inadequate, because over half of the seals found entangled in the less dangerous types of fishing gear (©database maintained by Metsähallitus, 2011; III) and 40% of the entangled pups studied in 1995–2012 (N = 5) were found outside the gillnet ban period. Furthermore, the average weight of a weaned pup is ca. 20 kg (Hyvärinen et al., 1998) and a recent dietary study has shown that the pups lose weight after weaning and up to end of the summer (Auttila et al., 2013). Light weight increases the by-catch risk for the pup (Hyvärinen & Sipilä, 1998; Sipilä, 2003).

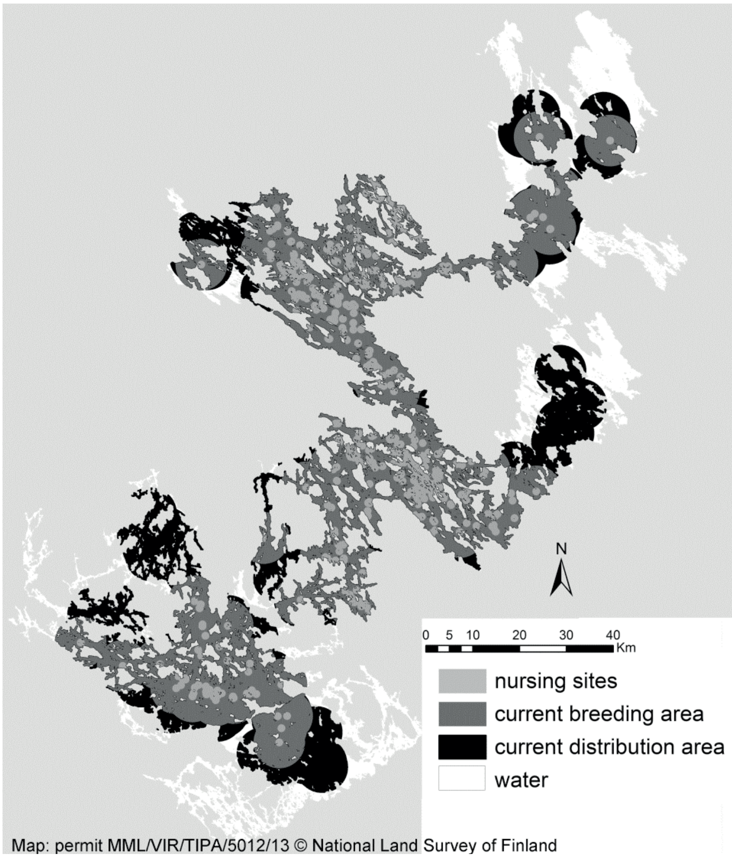


Figure 3. *Current distribution area, breeding area and nursing sites of the Saimaa ringed seal based on lair censuses and estimated home ranges of adults and pups (Article III).*

Given that pup survival is low in Lake Saimaa (Sipilä et al., 1990; Kokko et al., 1998), special attention should also be paid to the coverage of the year-round gear type restriction in addition to the spring-time restrictions, as former has up to now covered only 63% of the breeding area and 55% of the seals' current distribution area. According to the mortality records kept by Metsähallitus (2011), some pups and adults become entangled in the 'dangerous' types of fishing gear every year in spite of the gear type restriction (III). Adult mortality is the greatest factor affecting the rate of population growth (e.g. Goodman, 1981; Harding et al., 2007), thereby increasing the risk of extinction for this endangered seal population.

The calculated current breeding and distribution areas should be the minimum spatial requirement, when planning fishing restrictions. Even with the small number of animals studied here, there were notable differences in movement patterns between the individuals. We should therefore avoid excessive generalization and bear in mind that the differences in movement patterns may express differences in behavioural types or personalities. This has been an emerging topic in behavioural studies on animals in general (e.g. Bell, 2007; Bell et al., 2009) including pinnipeds (Twiss & Franklin, 2010; Twiss et al., 2012). Even if the restriction areas were based on the average home range sizes used evenly as buffers around the winter lairs, the seals living in the areas situated on the edge of the distribution, and individuals that make sporadic movements, would still be poorly conserved (Fig. 4).

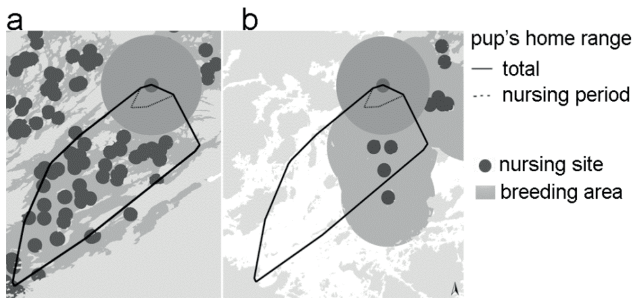


Figure 4. *To estimate nursing sites and breeding areas for the Saimaa ringed seals, buffers were drawn around their birth lairs using the average sizes of the pups' home ranges. The solid and dotted lines show the real home range areas of one pup situated in the hypothetical areas of Lake Saimaa. a) The whole home range area would be well conserved within the main breeding area, but b) on the periphery the seals may still be poorly conserved.*

Ecotourism can provide visitors with educational and highly positive experiences which may benefit wildlife conservation in the form of positive attitudes or contributions towards conservation measures (Zeppel & Muloin, 2008). It may also have negative side effects, however, such as intentional or unintentional damage to the native fauna (Isaacs, 2000). In order to mitigate anthropogenic disturbance in the case of moulting seals in particular, the present results should be used as an aid in the development of guidelines for seal watching in Lake Saimaa. Based on the response behaviour of the moulting seals, the median distance at which the seals did not response to the approaching boat (300 m; IV) could be considered a "safe" viewing distance. Compliance with this guideline may be unrealistic, however, due to the labyrinthine nature of Lake Saimaa. Therefore, attention should be focused especially on boating practices, as it is known to affect the response behaviour of seals (Allen et al., 1984; Suryan & Harvey, 1999; Andersen et al., 2012; IV).

In addition to the average figures, the variations in the seals' behaviour should be highlighted when discussing the choice of means of conservation. This could improve the acceptability of conservation measures, which may otherwise cause opposition among the local people, who have experience of certain types of behaviour among seals (Tonder & Jurvelius, 2004; Bell et al., 2008). In particular, it is claimed that the number of seals is higher than the estimates quoted by researchers, so that strict protection in form of fishing restrictions is thought to be unnecessary (Tonder & Jurvelius, 2004; Tonder, 2005). Such assumptions of higher population numbers may be a result of experiences which are genuine in themselves but skew the numerical implications, as the present results show that the seals are capable of making long sporadic movements, using very narrow channels and moving from one lake basin to another (III). This means that the same seal may be seen in two distinct areas in the course of the same day, creating the illusion that there are more seals in a certain area than is really the case.

4 Conclusions

Practical efforts for the conservation of threatened and endangered populations can be considerably enhanced by achieving a thorough understanding of the spatial ecology of the species concerned. This approach requires an extensive knowledge of movements, migrations, dispersal, site fidelity, and home range size as well as the seasonal spatial behavioural patterns of the species. Therefore, detailed information on the current and prospective distribution and behaviour of the Saimaa ringed seal is essential for efforts at conserving of this critically endangered population. This knowledge can be further developed for effective conservation measures in order to prevent the over-regulation of human activities.

This thesis not only offers implications for conservation, based on the behaviour of the seals, but also provides information on the behavioural ecology of a subspecies of ringed seal that may in some aspects be generalizable and useful for comparisons with marine subspecies. The movement patterns of Saimaa ringed seals are similar to those of ringed seals in a marine environment, being characterized by individual variation (e.g. Gjertz et al., 2000; II, III, IV), mobile juveniles (Kunnasranta, 2001; Freitas et al., 2008; II), sporadic movements on the part of some adults (e.g. Gjertz et al., 2000; Kelly et al., 2010a; III) and site fidelity (Smith & Hammill, 1981; Teilmann et al., 1999; Kunnasranta, 2001; Koskela et al., 2002; Sipilä, 2003; Kelly et al., 2010a; Valtonen et al., 2012; III, IV). The main differences are matters of scale and structure, and also of the levels of anthropogenic disturbance in Lake Saimaa and in marine environments. Additional behavioural data would be needed to study GPS-based fine-scale movement patterns for the pups and over-yearlings, foraging, seasonal and regional behaviour patterns, and hypotheses regarding differences between the sexes in order to further understand the behavioural ecology of the Saimaa ringed seal and to continue to develop effective conservation measures.

The main conservation implications in this thesis were the definitions of the nursing sites (I, II & III), breeding area (II & III), current distribution area (III) and description of the haulout behaviour (IV) of the Saimaa ringed seal. This information should further enhance implementation of the relevant EU legislation and compliance with the national legislation.

The natal site is actively used by the mother-pup pair until the dispersal of the pups in mid-May (I, II). Therefore, these sites, including the home ranges of the pre-weaned pups (III), should be subject to conservation in all aspects, including land use on the shores, water-level outflow, fishing restrictions and off-road traffic, to minimize disturbances, especially during the breeding time in winter. To further mitigate the anthropogenic disturbance, guidelines for seal watching should be developed based on the responses of the seals to motorboat traffic during the moulting period (IV). Also, the haulout areas of the seals should be identified and conserved by means of sustainable land use planning.

After their dispersal the pups explore surrounding habitats, moving more and establishing larger home ranges than has previously been suggested (II). The main conservation implication based on the home ranges of the pups was the determination of breeding areas for the whole of Lake Saimaa (III). To improve juvenile seal survival, these data should be taken into account when planning both the spatial and temporal coverage of the spring-time fishing restriction (government degree 294/2011). Furthermore, the adult seals' home ranges were large, mostly due to sporadic movements, the main conservation implication in this respect being the determination of the distribution area of the Saimaa ringed seal (III). To improve the survival of both juvenile and adult seals, these data should be taken into account when planning the spatial coverage of the year-round fishing restrictions (government decree 295/2011).

5 *References*

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Marja Niemi

Behavioural ecology of the Saimaa ringed seal – implications for conservation

Saimaa ringed seal is a subspecies inhabiting the fragmented Lake Saimaa in south-eastern Finland. The main threats for this critically endangered population are by-catch, destruction of suitable breeding habitat, small population size and climate change. This thesis brings new information on vocalization, movement patterns, home ranges and haulout behaviour of the Saimaa ringed seal and provides implications for conservation.

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