Dissertationes Forestales 214

Conservation biology of the great crested newt in managed boreal forests in Finland

Ville Vuorio

School of Forest Sciences

Faculty of Science and Forestry

University of Eastern Finland

Academic dissertation

To be presented, with the permission of the Faculty of Science and Forestry of the University of Eastern Finland, for public criticism in the auditorium N100 of the University of Eastern Finland, Yliopistokatu 7, Joensuu, on April 1st 2016, at 12 o’clock noon.

Title of dissertation: Conservation biology of the great crested newt in managed boreal forests in Finland

Author: Ville Vuorio

Dissertationes Forestales 214

http://dx.doi.org/10.14214/df.214

Thesis Supervisors:
Professor Jari Kouki
School of Forest Sciences, University of Eastern Finland, Finland
Docent Olli-Pekka Tikkanen
School of Forest Sciences, University of Eastern Finland, Finland

Pre-examiners:
Professor Anssi Laurila
Animal Ecology/ Department of Ecology and Genetics, Evolutionary Biology Center, Uppsala University, Sweden
FNRS Senior Research Associate Mathieu Denoël
Behavioural Biology Unit, University of Liege, Belgium

Opponent:
Academy professor Juha Merilä
Ecological Genetics Research Unit, Department of Biosciences, University of Helsinki, Finland

ISSN 1795-7389 (online)
ISBN 978-951-651-518-5 (pdf)

ISSN 2323-9220 (print)
ISBN 978-951-651-519-2 (paperback)

Publishers:
Finnish Society of Forest Science
Faculty of Agriculture and Forestry of the University of Helsinki
School of Forest Sciences of the University of Eastern Finland

Editorial Office:
Finnish Society of Forest Science
P.O. Box 18 FI-01301 Vantaa, Finland
http://www.metla.fi/dissertationes

Vuorio, V. 2016. Conservation biology of the great crested newt in managed boreal forests in Finland. Dissertationes Forestales 214. 45 p.
http://dx.doi.org/10.14214/df.214

ABSTRACT

This study focuses on the population and behavioral ecology of the endangered great crested newt in its natural forest habitat in Finland. I also explored the characteristics of the smooth newt and compared the two species. They are closely related but occur with different abundances in the same environments.

Hatching success and survival of eggs were modelled using a combination of field and literature data. Eggs that were laid in the early season produced the best hatching results. This success rate dropped dramatically in combination with a decreasing water level. Terrestrial habitat characteristics, such as the amount of herb-rich forests, clear-cuts and broad-leaved trees, were related to the breeding success of the newts. Both newt species distinctly favored forests with high understory vegetation cover. Both the common and the rare species showed largely similar habitat use, however the rare species avoided clear-cut areas and was more abundant on sites where shelter was provided by the canopy and field-layer vegetation, especially when the distance to the pond increased.

Four spatially and temporally different habitat and landscape scenarios were explored to model the extinction and colonization dynamics of the great crested newt. Intensified timber harvest and a shorter logging rotation were shown to decrease the connectivity between ponds.

Overall, the results suggest that particular attention should be paid in conservation planning to the spatial arrangement of the habitat patches, especially if the intensity of the human impact is predicted to increase. The conservation effort must be targeted at securing the source ponds in the core area and the enhancement of connectivity between the habitat patches of the newts. As the hatching success of the great crested newt is strictly regulated by climatic factors, temperature and water level, a considerable future threat for the species might come with climate change.

Keywords: oviposition, hatching, breeding success, terrestrial habitat selection, inter-pond matrix

ACKNOWLEDGEMENTS

If you brew for the first time, you really don’t know when to bottle the beer. You know that the fermentation is approaching the end when the bubbling interval in the airlock gets longer. But what is the optimal bubbling interval? If you bottle the product too early, the fermentation continues in the bottle. The gas inside the bottle will break the bottle at the weakest point. But, on the other hand, if you wait too long after the fermentation has finished, the yeast starts to give flavor to the final product. As brewing is both a science and an art, there is nothing absolute. You just have to brew, taste, learn and replicate. The fascination in brewing is the search for the perfect recipe. I’m pretty sure that the best beer ever has not been brewed yet. A brewer knows that he/she might never find the recipe for the best beer, but it is still worth searching for it.

When you do your (first) PhD, you really don’t know when to close the cap. If you close it too early, your opponent starts to crack the product from the weakest point. On the other hand, if you wait too long, the same happens as in brewing; the taste of yeast starts to take over and you don’t want to touch it. Here I have made an attempt to “approach” the truth. I did not even dream that I would find it. Approaching was the best I could do. In brewing, the beer is not ready after closing the cap. The final character, body and flavors develop with proper maturation. Now I’m leaving this thesis for maturation, dear reader. I warn you not to try to find the truth here. However, I hope that the character, body or after taste of this publication will inspire you to take on this kind of work and further advance our knowledge in this field of research.

Funding for this thesis was provided from the Maj and Tor Nessling Foundation (grants 2010230, 2011277, 2012211, and 2013089) and the Finnish Academy of Sciences (decision 263465, Water management and peat production: from relevant facts to effective norms), and are gratefully acknowledged for their support. European Journal of Forest Research as well as Finnish Zoological and Botanical Publishing Board are thanked for granting the permission to include published articles to this work.

I worked under the guidance of Prof. Jari Kouki and Docent Olli-Pekka Tikkanen from the School of Forest Sciences in the University of Eastern Finland. I thank them warmly for all their guidance and help during the work. Olli-Pekka was one of the main reasons that I started this PhD. The original idea to undertake a PhD study on newts came from him about eight years ago. I’m grateful that he was always available and supportive during the whole process: planning, fieldwork, data analysis and writing. I’m also very, very grateful to all my co-authors for their highly intellectual and practical contributions: Ari Láuren, Lauri Mehtätalo, Pasi Reunanen, Risto Heikkinen, Olli-Pekka Tikkanen and Jari Kouki. Without them this work would not have been possible. I’m also very grateful for the valuable comments from several people who commented on the manuscripts, even when they were not a co-author: Jari Kouki, Pasi Reunanen and Teemu Tahvanainen. For Teemu, special thanks for reminding me to have fun as well; I have hidden two special words for you in the text. I have been lucky enough to have excellent assistants during field work: Riikka and Raisa worked long days in data collection somewhere in Öllölä, Mar helped in the egg count in rain and sunshine, numerous biology and forestry students, together with the parents from the Steiner school of Joensuu dug and erected more than two kilometers of fences.

There are also numerous other people outside the box, who have given me food for thought and thus balanced my life during this work. The work *an sich* was not always rewarding, smooth or easy. In that respect, I suppose, the work imitates life itself. I want to express my gratitude to my lovely wife Krista Mikkonen and kids Ilmo, Oiva and Aimo, who have been my number one priority all the time. Thanks also to my mother and sister for their support. There are many friends who have given me inspiration in one way or another. Jani and I have so far brewed, fished and done weird things, Pekka has been there to give support in fatherhood, baking nights and board games, Sami has always been ready to run under different circumstances, Jusa has offered visual perspectives and cigars, Veli has been fixing our boat, Tapio has offered good conversations while running (also when not running). Many thanks also to Krisse, Teemu, Kaisa, Harri, Hanna, Helena, Bosse, Katarina and all our joyful Ilosaarirock guests over the last 20+ years who have provided the best weekend of the year: Kati, Erkka, Pekka… A special thanks also to all my friends at the Department of Biology in the 1990s. This group formed a mental base camp. Thanks also to the other PhD-students at the School of Forest Sciences. With this kind of background, penetrating the gray scientific concrete did not hurt so much.

Joensuu, March 2016
Ville Vuorio

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles, which are referred to in the text by the Roman numerals I–IV. This thesis is a summary of the following articles, which are referred to in the text by the Roman numerals I–IV. Article I is the authors' version of a submitted manuscript. Articles II, III and IV are reprints of previously published articles reprinted with the kind permission of the publisher.

I Vuorio, V., Tikkanen, O.-P., Laurén, A. (2015). Survival of newt eggs in variable abiotic conditions in boreal ponds. Manuscript.

II Vuorio, V., Heikkinen, R. K., Tikkanen, O.-P. (2013). Breeding success of the threatened great crested newt in boreal forest ponds. Annales Zoologici Fennici 50: 158-169.
http://www.sekj.org/PDF/anz50-free/anz50-158.pdf

III Vuorio, V., Tikkanen, O.-P., Mehtätalo, L., Kouki, J. (2015). The effects of forest management on terrestrial habitats of a rare and a common newt species. European Journal of Forest Research 134: 377-388.
http://dx.doi.org/10.1007/s10342-014-0858-7

IV Vuorio, V., Reunanen, P., Tikkanen, O.-P. (2016). Spatial context of breeding ponds and forest management affect the distribution and population dynamics of the great crested newt. Annales Zoologici Fennici 53: In press.

Author's contributions

Article	I	II	III	IV
Original idea	AL, VV	O-PT, VV	O-PT, VV, JK	PR, O-PT, VV
Study design	VV	O-PT, VV	O-PT, VV	PR, O-PT, VV
Data collection	VV	VV	O-PT, VV	VV
Data analysis	AL, O-PT, VV	RHK, VV	JK, LM, VV	PR, O-PT, VV
Manuscript preparation	AL, O-PT, VV	RHK, O-PT, VV	JK, LM, O-PT, VV	PR, O-PT, VV

RKH, Risto K. Heikkinen; JK, Jari Kouki; AL, Ari Laurén; LM, Lauri Mehtätalo; PR, Pasi Reunanen; O-PT, Olli-Pekka Tikkanen; VV, Ville Vuorio

CONTENTS

1 INTRODUCTION

1.1 Amphibians in changing world

The global decline of numerous amphibian species has been widely documented (Houlahan et al. 2000, Stuart et al. 2004, Lips et al. 2006, Pounds et al. 2006). The decline has been linked to the loss and degradation of terrestrial and aquatic habitats (Stuart et al. 2004, Beebee and Griffiths 2005), poor dispersal abilities (Sinsch 1990, Gibbs 1998, Kovar et al. 2009), diseases, introduced species (Beebee and Griffiths 2005, Denoël and Lehmann 2006, Denoël and Ficetola 2008), high mortality rates in inhospitable terrains (Fahrig et al. 1995, Carr and Fahrig 2001, Stevens et al. 2006, Eigenbrod et al. 2008, Cosentino et al. 2011), and a fairly narrow tolerance of abiotic conditions (Semlitsch 2000, Houlahan and Findlay 2003) which also makes amphibians vulnerable to changes in terrestrial habitats.

Habitat connectivity has been proposed as the main factor determining survival of viable populations at the regional level (Hanski and Ovaskainen 2000, Eycott et al. 2012, Van Buskirk 2012). In fragmented landscapes, the low recruitment of dispersing individuals has been thought to play a major role in the decline and extinctions of amphibian populations (Vos and Chardon 1998, Bulger et al. 2003). The importance of connectivity for habitat recolonization by local amphibian populations is documented in many cases (Skelly et al. 1999, Trenham et al. 2003, Gould et al. 2012). While structural connectivity refers to the spatial arrangement of different habitat types in a landscape, functional connectivity addresses the behavioral response of individuals to the physical structure of the landscape (Wiens 2006).

In Europe, 59 % of amphibian species have declining populations, and nearly a quarter of amphibian species are considered threatened (Houlahan et al. 2000, Denoël and Ficetola 2008, Temple and Cox 2009). The main drivers of the decline are habitat loss and degradation, as indicated by the fact that more than 60 % of freshwater habitats have an unfavorable conservation status in Europe (European Commission 2009, Temple and Cox 2009).

Many amphibians spend part of their life cycle in terrestrial habitats, while breeding may take place in aquatic habitats. Thus, amphibian species that live in small water-bodies in forested landscapes are affected by the management of the surrounding forests. For example, intensive harvest operations (thinning and clear-cutting) may profoundly change the abiotic conditions of the forests. If management also includes soil preparation measures, these may affect the dispersal and overwintering of amphibians directly. Forest thinning causes changes in tree species composition and forest floor properties, such as the amount of dead wood and composition and coverage of understory vegetation. Clear-cuts result in more dramatic consequences and lead, in many cases, to large-scale habitat modification and may also cause direct mortality by forestry machines (Bol 2007). At the landscape level, habitat fragmentation caused by forest management reduces the size of habitat patches and increases patch isolation and, hence, extinction risk through the reduction of genetic and demographic input from immigrants (Lande 1988, Gulve 1994, deMaynadier and Hunter 1998).

Breeding ponds are typically seasonally dynamic or even ephemeral habitats. In amphibians, the facilitation of connectivity is, thus, of primary importance because a pond might desiccate in summer due to dry weather conditions and a high connectivity facilitates the recolonization of ponds. In recent decades, human activities have resulted in massive changes at the landscape level with the expansion of transportation networks, agriculture and urban areas. For many species, this means a reduction in the quality and quantity of the habitat and matrix (Fahrig 2007). Intervening areas between the ponds are homogenous and unsuitable only in the most heavily modified landscapes. Often, a matrix is a composition of a variety of habitats of varying quality (Wiens 2006).

Many amphibian studies have shown that the presence or abundance of a species correlates with the distance to the nearest forest (Guerry and Hunter 2002, Weyrauch and Grubb 2004, Rannap et al. 2012). This relationship is typical in human-dominated landscapes (Guerry and Hunter 2002) where the habitats adjacent to ponds are normally comprised of a mixture of fields, grazed fields, gardens, woodland pastures and forest patches. In natural landscapes, though, the pond network is often embedded in a forested matrix. However, a forest is not a homogenous environment for the newt. The quality of a forest as a migration route through terrestrial habitats varies due to natural variations in vegetation cover or as a result of forest management activities (Patrick et al. 2008).

1.2 Study species

The studied species belong to the subfamily Pleurodelinae of the family Salamandridae. The distribution of the great crested newt, *Triturus cristatus* (Laurenti, 1768) covers most of central Europe reaching southern Scandinavia and the Baltic countries. In the east it extends as far as south-western Siberia (Arntzen et al. 2009b). The distribution area of the smooth newt, *Lissotriton vulgaris* (Linnaeus, 1758) is wider and covers most of Europe, excluding the Iberian Peninsula. In the north is reaches further into Scandinavia and extends further east into Russia than the great crested newt (Arntzen et al. 2009a).

The annual life cycle of both species involves the usage of both terrestrial and aquatic habitats. Ponds are used for breeding and foraging and they serve as a larval habitat. Larvae live only in ponds until they develop into metamorphs. The best breeding ponds are fishless and relatively nutritious, with a pH above 5. Adult newts spend most of their life cycle in terrestrial habitats, which are used for dispersal, hibernation and foraging. Preferred terrestrial habitats are covered by vegetation; with the shelter provided by understory vegetation especially important. Open sites are avoided (Halley et al. 1996, Jehle and Arntzen 2000, Gustafson et al. 2009, Vuorio et al. 2013, Vuorio et al. 2015). Both species share similar seasonal and daily activities. However, the smooth newt has a wider pH tolerance, it has a considerably smaller body size than the crested newt, it can breed in smaller water bodies that may dry out seasonally, and can also breed in larger lakes in the presence of fish (Dolmen 1988).

There is a local overlap in the distribution and habitats of the two species, and both are generalist predators (Griffiths and Mylotte 1987, Skei et al. 2006). They occur sympatrically in northern European forest ponds (Denoël et al. 2013). However, their distribution and areas of occupancy are quite different. In Finland, the crested newt has a very restricted distribution of 16,600 km^2 (minimum convex polygon) in the east and south, while the smooth newt is much more widespread and is distributed over 212,000 km^2 (Arntzen et al. 2009a, Arntzen et al. 2009b, Vuorio 2009, AmphibiaWeb 2014).

Newts have a characteristic pattern of seasonal movement between their terrestrial hibernation sites and the aquatic breeding sites and may be highly dependent on the quality of the terrestrial habitats providing access to these sites (Van Buskirk 2005, Patrick et al. 2006). Semlitsch (2008) defines the primary adult amphibian migration as “reoccurring movements from overwintering sites to ponds to breed in addition to the return of females and males to terrestrial habitats”. Migrations may also occur between overwintering sites, foraging areas, and summer habitats (Lamoureux et al. 2002, Semlitsch 2008). Typically, the migration of adults is non-random; they enter and exit the pond in the same place and have a preference for particular travel routes (Müllner 2001, Sztatecsny and Schabetsberger 2005, Rittenhouse and Semlitsch 2006, 2007, Freidenfelds et al. 2011).

The great crested newt has been included in Annexes II and IV of the European Habitats Directive and has received a Species Action Plan (Edgar and Bird 2006). This status calls for intensive research on the environmental factors that govern the distribution and abundance of newt populations, which is a prerequisite for effective conservation and management planning (Edgar and Bird 2006, Denoël and Ficetola 2008, Gustafson et al. 2011). In Europe, the species is currently classed as critically endangered in the Czech Republic (Vlašín 2003), Austria (Gollmann 2007) and Belgium (Belgian Species List 2015), endangered in Finland (Terhivuo and Mannerkoski 2010), Switzerland (Schmidt and Zumbach 2005), Hungary (Vlašín 2003) and Slovakia (Vlašín 2003) and vulnerable in Norway (Dolmen 2010), Estonia (Red Data Book of Estonia 2008), the Netherlands (Creemers 2003) and Romania (Cogălniceanu and Rozylowicz 2015). Though the species is rare and has clearly declining populations in many parts of its distribution, it may still remain relatively common in suitable habitats (Arntzen et al. 2009b, Denoël 2012).

1.3 Aims of the research

Although the great crested newt has been the subject of several studies (Edgar and Bird 2006, Karlsson et al. 2007, Denoël and Ficetola 2008, Gustafson et al. 2011), our knowledge of the species’ habitat requirements is still incomplete. First, the majority of the studies have been conducted in Central and Western Europe, where the species occurs in a human-modified landscape that is affected by agricultural intensification, expansion of infrastructure and fish stocking (e.g. Joly et al. 2001, Edgar and Bird 2006, Denoël and Ficetola 2008). In these studies, the quality of forested vegetation on the surrounding breeding ponds has rarely been investigated in detail. In Fennoscandia, the species occurs at its northern range margin and generally occupies a forest-dominated landscape where the factors affecting the distribution and abundance of the newts are likely to be different, in comparison with the southern European populations (Gustafson et al. 2006, Skei et al. 2006, Gustafson et al. 2009, Gustafson et al. 2011).

Second, several modeling studies on amphibians and their relationships with habitat factors have employed presence-absence data (e.g. Pellet et al. 2007, Denoël and Ficetola 2008, Gustafson et al. 2009, Hartel et al. 2010, Gustafson et al. 2011, Gomez-Rodriguez et al. 2012; but see Joly et al. 2001; Denoel and Lehmann 2006). Presence-absence data are useful to assess distribution patterns of species and to detect changes in them. However, such data provide little understanding of the spatial and temporal dynamics in local populations (Beebee and Griffiths 2005). Furthermore, presence-absence models do not distinguish poor habitats from higher quality sites with more abundant populations, which is important in conservation planning (Denoël and Lehmann 2006). Third, where abundance data of the amphibians have been employed in the analyses, often only adult individuals have been considered (e.g. (Joly et al. 2001, Denoël and Lehmann 2006). Improved understanding of the sites with the highest reproductive potential can be better achieved using estimates of abundance of juveniles (Knutson et al. 2004). Such information provides more detailed estimations of the populations' long-term persistence dynamics and local population dynamics than number or density of adults alone.

In this work I have tried to fill the knowledge gap in regard to the ecology of the great crested newt in northern Europe. I have studied all the life stages of the newt from egg to adult. My study domain has covered both aquatic and terrestrial habitats as well as different temporal periods.

The study is based on four articles (referred hereafter as **I**, **II**, **III** and **IV**). The focus of the first article was to determine the effects of water level fluctuation and temperature on newt egg survival. In addition, I recorded new data in regard to the northern ecology of the newts, temperature preferences in relation to arrival at the pond, plant selection and the temperature range of oviposition.

The main research questions in article **II** were to determine (a) how terrestrial habitats affect the breeding success of the great crested newt, and (b) how accurately can breeding success be modeled using existing forest inventory data, in order to support the creation of suitable breeding ponds elsewhere? In addition, I investigated how well the breeding success of the great crested newt can be explained by simply using the size and isolation of a given pond.

Article **III** focused on the differences in terrestrial habitat use between the common smooth newt and the rare crested newt. I tried to clarify the responses of the two sympatric newt species to terrestrial habitat change, in particular to changes caused by intensive forest management. I hypothesized that the rare newt species would have a narrower use of habitats (intolerant) and to be affected more by forest management actions than the common one. Therefore, I asked a specific question “do the rare and common species differ in their occurrence patterns, in relation to the quality and structure of managed forests (age, fertility, cover of canopy and field layer) that surround breeding ponds?” I also wanted to know whether there is a change in the occurrence pattern of the two species in forest stands that are more distant from the pond; that is, are the buffer zone requirements similar for the common and rare species?

Finally, in article **IV**, I modelled the future prospects of this endangered species. Using detailed and fine-grained forest inventory data, literature sources and empirical field data from previous studies over a ten year period, I constructed a spatially explicit population model for the great crested newt in a boreal forest landscape. I studied the effect of temporal change on land-use intensity and landscape change on the population dynamics in four spatial data sets. Based on the analysis, I discuss meaningful management schemes to ensure the persistence of the breeding ponds and the ecological connectivity of breeding habitats at the landscape scale.

2 MATERIALS AND METHODS

2.1 Study area

In Finland, the great crested newt has a disjunctive distribution separated by a 400 km wide gap: (1) the region of Åland in the south-western archipelago with circa 30 breeding ponds and (2) eastern Finland with 70 breeding ponds. Articles **I** – **IV** concentrated on the central parts of the mainland distribution area located in eastern Finland, which has the highest density of known breeding ponds nationally. The most extensive area was covered in article

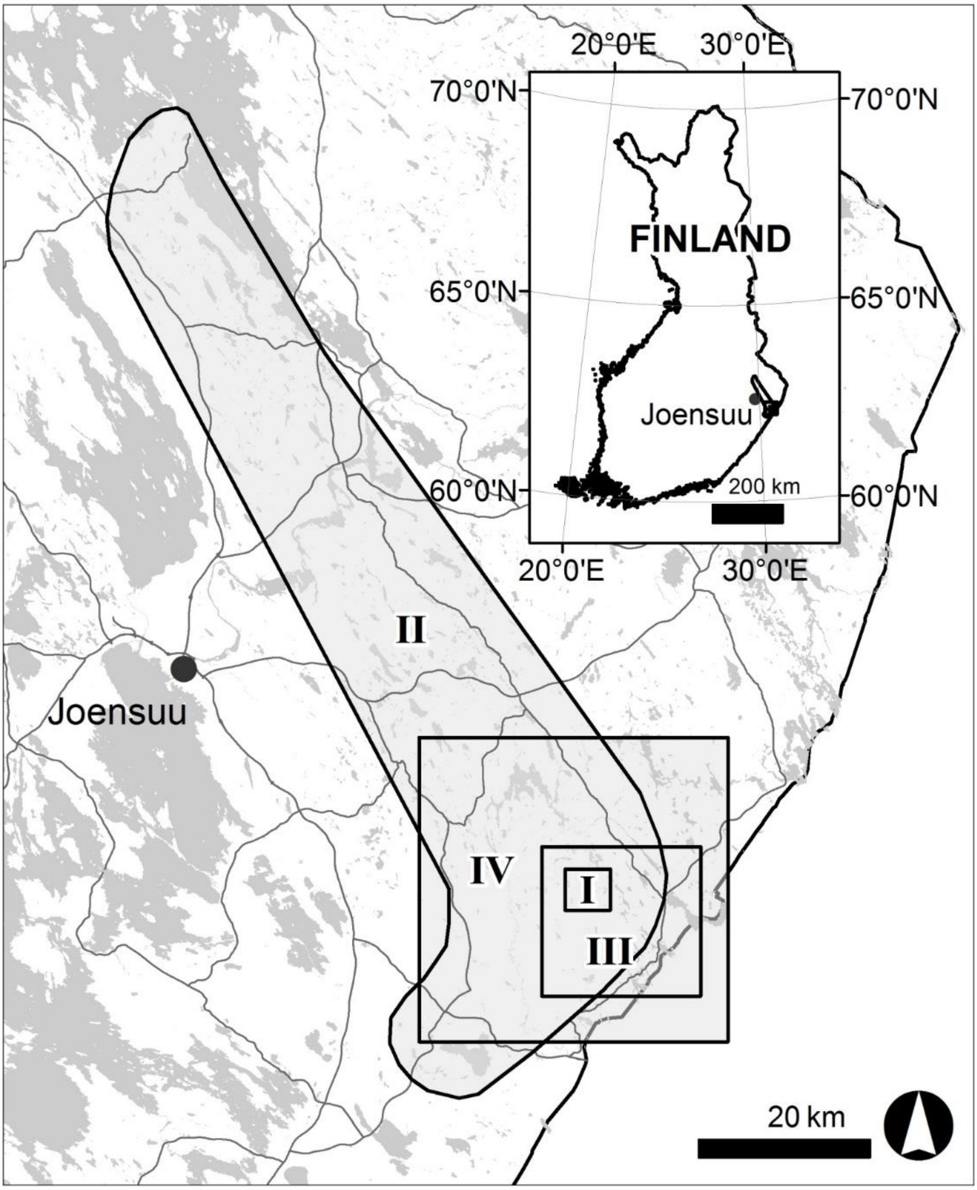

Figure 1. Study areas. The exact location of individual breeding ponds of the great crested newt is not public information. Therefore, the map shows the approximate areas only. ©Digiroad 2015, ©Maanmittauslaitos, ©SYKE.

II, which extends from the municipality of Tohmajärvi (62°10”N, 30°19”E) 120 km NNW to the Koli region (63°11”N, 29°49”E) as a 20-25 km wide belt (Fig. 1) at 80-347 m elevation above sea level.

Eastern Finland is sparsely populated, dominated by wide-ranging boreal coniferous forests (i.e. 89.5 % of the total land area of North Karelia) and peatlands (Metla 2012). Landforms are characterized by the Tuupovaara end moraine, an ice-marginal formation that evolved during the period of a freshwater Baltic Ice Lake 12,600–10,300 BP. Ponds in the study area largely originated from glacial processes, where large pieces of ice split from the retreating glacier and formed depressions when melting (Rainio 1983, Tikkanen and Oksanen 2002). The area is characterized by sporadic, small groundwater-fed ponds, which act as breeding areas for the newts (Vuorio 2009). Biogeographically, the study area mainly belongs to the southern boreal vegetation zone, as only the northern portion extends to the middle boreal vegetation zone (Ahti et al. 1968). The annual mean temperature in the study area (1981-2010) is 2-3 °C and precipitation is 650-700 mm/year. The thermal growing season starts around May 2-7 and has a typical length of 155-165 days (Finnish Meteorological Institute 2015).

Since the second half of the 20th century, forests have been intensively managed for timber production, based on clear-cuts, soil scarification, planting or seeding new tree cohorts, and subsequent thinnings. Prior to this period, forests were commonly used for slash-burning (Heikinheimo 1915). Slash-and-burn sites were abandoned after a few years and left to regenerate naturally (Björn 1991). Currently, the vast majority of forests are commercially utilized and the known breeding ponds of the crested newt have a 75 m wide buffer zone where logging is restricted.

2.2 Methods

2.2.1 Oviposition, I

I studied the spatial and temporal distribution of newt eggs in four ponds under the following criteria: the pond was a known breeding area for the great crested and smooth newts, no drainage ditches were present, previous data from the pond was available (**II** and **III**) and they were forest ponds with a natural water level fluctuation. I placed two 1m wide transects across each pond starting at the shore line and extending to the center of the pond. The first transect was placed at the site where the first egg was found. The starting point for the second transect was placed at least 5m away from the first transect and extended to the site where the next egg was found.

Transects were checked by examining each transect from both sides so as not to disturb the transect itself. When a newt egg was found, the plant that the egg was laid on was recorded and identified by dropping a piece of white plastic with a running number and an attached weight to the base of the plant. The following were then noted; identity of the plant, whether the plant was dead or alive, the distance from the plant to the shore, the distance from the bottom of the pond to the egg and the distance from the egg to the surface of the pond. In subsequent visits only new eggs were counted. I measured the water temperature in the middle of the ponds using four data loggers (Hobo Pendant temperature/light 64 K data logger, Onset Computer Corporation) per pond at the depths of 10, 20, 40 and 80 cm. The temperature was recorded at one hour intervals. Water level was measured at the same time intervals using water level loggers (Hobo water level logger U20-001-01, Onset Computer Corporation), which were placed at the deepest point in each pond.

2.2.2 Breeding success, II

The initial 70 great crested newt breeding ponds were assigned to three groups each containing 23-24 ponds, according to their average breeding success in 2005-2009. From each of these three groups, 15-16 ponds were randomly selected for more detailed data collection. I collected data on forest mensuration, forest type in the vicinity of the ponds and several other pond characteristics, such as vegetation, pH, depth, pond bottom type and shading. The total number of selected ponds was 46, which were then re-surveyed twice using dip-netting to capture larvae (Briggs et al. 2006, Skei et al. 2006, Skelly and Richardson 2010). A standard dip-netting method employs a 2m sweep at the shoreline. During the seven years (2005-2011) of data collection, each pond was visited on average 4.98 (±0.27 *SE*) times. During each visit, sweeping was repeated on average 28.4 (±0.95) times in each pond. Dip-netting was always done once per pond at the beginning of August.

The number of ponds sampled each year varied from 21 to 46 due to pond's drying up and locating new breeding sites during the study. Breeding success is reported as the number of larvae caught per dip-net/ pond/ year. As the proportion of the sampled area out of the total pond area varied between ponds, the value for breeding success is not an explicit measure of the size of the larval population but an indicator of the overall breeding success of a pond.

2.2.3 Terrestrial habitat use, III

I mapped the terrestrial habitats, i.e. delineated the forest compartments of 46 ponds (see article **II** for details) where both newt species were known to breed. Eight of the ponds were selected for the drift fence study following two criteria: each pond should have at least three different terrestrial habitat types in the vicinity and the ponds should be relatively close to each other for logistical reasons. The selected ponds originated from glacial processes and varied in area between 390 and 3700 m^2. I delineated the surroundings of each pond into three 25m wide zones that extended up to 75 m, starting from the shore line of each pond (Fig. 2). The forest compartments at different distance zones formed the study units. Each of the six selected habitat types occurred at least three times within each of the three distance zones: 0 – 25 m, 25 – 50 m and 50 – 75 m. The only exception was in the number of clear-cuts; they were found only once in the first zone and twice in the second and third zones. Within each study unit, I randomly placed one to four traps. Each trap consisted of a drift fence that was 2–10 m long. The capture effort per area remained the same in each of the study units: 1 m of fence / 60 m^2.

The trap fences were made from 40cm wide green plastic tarpaulin strips. The lower edges of the strips were buried 5–10 cm underground and the fence was erected using metal stakes and cable ties. Fences were always parallel to the tangent of the closest point of the shoreline. Both ends of the fence had a 5L bucket inserted into the ground so that the rim reached the soil level. Buckets were half filled with water. Traps were checked once a day during the whole study period.

The breeding season started at the beginning of May when the ice cover over the ponds melted. The sampling period targeted the post-breeding migration prior to post-metamorphic migration. During 2010, I operated 132 traps (a total of 1135 m of fences). Trapping started on 1 June 2010 and ended on 30 June 2010. In 2011, trapping started on 9 June and ended on 20 July, with 135 traps operated (1130 m of fences). The different periods of data collection were taken into account in the data analyses, and recaptured newts were also excluded from the dataset.

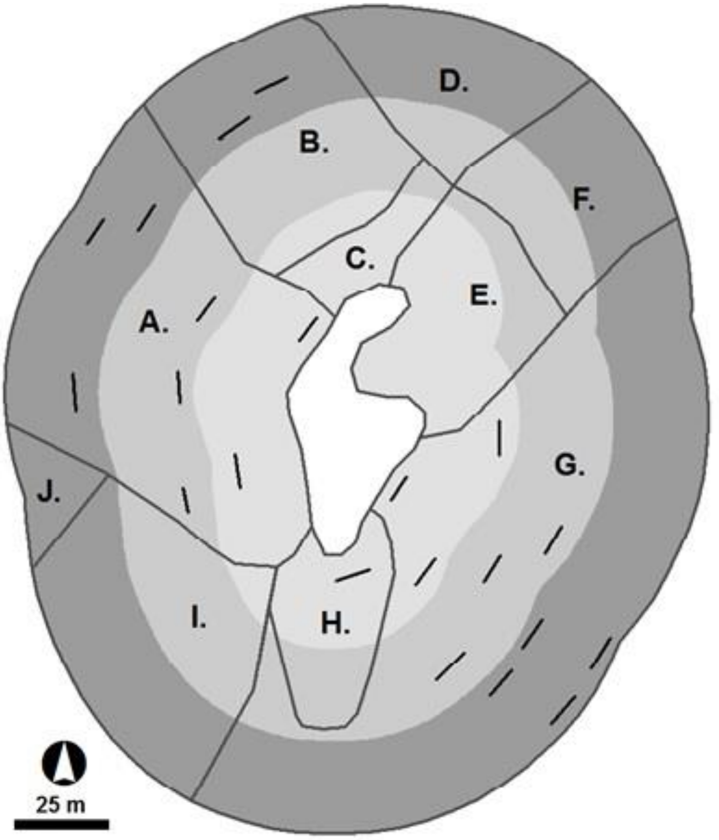

Figure 2. Schematic map showing the study setting (article III) in one of the studied ponds. Letters A.-J. indicate different habitat types. Three shades of grey indicate the distance from the pond in 25 m intervals. Fences are marked as black lines.

From each trapping unit, I collected compartment level data on canopy age and cover together with ground layer vegetation cover and nutrient levels. I placed on average 4.6 (± 0.170) plots / m^2 (808 in total) in each compartment to study the coverage of forest type indicator species (Hotanen et al. 2008).

2.2.4 Connectivity, IV

Four landscape scenarios were constructed to illustrate the anthropogenic impact on the environment: the historic landscape, the current managed landscape and two future scenarios. The landscapes form a gradient of land-use intensification. The historic landscape represents conditions before the start of intensive human activities; no permanent fields, loggings, roads, ditching or fish stocking of the smaller (< 1 ha) ponds. During this time, there were an estimated 163 ponds in the area. For this exercise, I assumed that the ponds contained fish as they were naturally connected to lakes by rivers or brooks. The rest of the ponds (unconnected), are considered to have been free from fish because they were formed on supra-aquatic land after the retreat of continental ice or due to desiccation (Rainio 1983).

The second landscape scenario represents the current landscape (as of 2011) with 183 ponds and represents an increase of 20 new ponds in comparison to the historic landscape. Four of the new ponds were excavated to mitigate the habitat loss of the great crested newt, while the rest were dug mainly for fish cultivation. All forests are commercially utilized; most of the peatlands are ditched, and there are roads, settlements and fields. Most importantly, fish have been stocked or spread widely in many ponds.

The future landscape scenario visualizes the study area in 2111. This scenario has two forest use variants, one with an 80-year logging rotation (future A) and another with a shortened 60-year rotation (future B). This scenario was used to simulate the predicted effect of climate change on tree growth and the impact of a new lower regulatory forest management approach. The typical and recommended management of Finnish forests is based on clear cuts and tree plantation, one or two thinnings and a final harvest of the forest stand at 80 years of age (Yrjölä 2002).

My main source of spatial data was the 11th Multi-source National Forest Inventory of Finland (MSNFI) compiled by the Finnish Forest Research Institute (Finnish Forest Research Institute 2013). The data set of MSNFI is processed from field survey data, high-resolution satellite imagery, digital land-use maps and elevation models. As a result, there are several thematic raster maps available at 20 x 20 m resolution. From the MSNFI data, I used the following raster maps: stand age, site fertility class and soil type.

MSNFI data was supplemented by the data of fields (Maaseutuvirasto 2009), roads (Liikennevirasto 2012) and water bodies (SYKE 2013). Based on these data sets, I compiled relevant landscape layers for the great crested newt.

2.3 Analysis

2.3.1 Oviposition, I

The temperature sum required from egg laying to hatching was modelled using laboratory data from literature sources (Griffiths and Dewijer 1994, Kinne 2006, Cvijanovic et al. 2009). A temperature sum function (Eq. 1) was fitted to the data by adjusting the threshold temperature:

$$H = 0.2638x^2 - 6.6689x + 56.509 \ (R^2 = 0.9193) \qquad \text{(Eq. 1)}$$

Where H is the time required from egg laying to hatching (days), x is the effective temperature of the water at egg depth with a threshold value of 8.6 °C. The temperature curve for each pond and each date was fitted separately using the measured temperatures at 10, 20, 40 and 80 cm depths. Using the combination of hatching equation and temperature curves, I estimated the hatching date of each egg. I also measured the water level changes in the pond. If the water level lowered more than the vertical distance between the egg and bottom of the pond, the egg was considered to have dried up. Using this approach I was able count the number of eggs that stayed submerged until hatching. The flow chart of deduction is presented in Fig 5.

2.3.2 Breeding success, II

I used generalized additive models (GAMs) to model the breeding success of the newt, by using calibrated breeding success as a response variable and the selected habitat characteristics as predictor variables. I applied the Gaussian probability distribution in GAM, which is a non-parametric extension of generalized linear models. GAMs are especially useful for detecting and describing nonlinear species-environment relationships (Hastie and Tibshirani 1986, Austin 2002). Following Denoël and Lehmann (2006), GAMs were mainly performed via the user interface GRASP (Generalized Regression Analysis and Spatial Prediction, Lehmann et al. 2003) embedded in S-PLUS (version 6.1 for Windows, Insightful Corp.). Prior to modeling, the correlations between the seven candidate predictors were tested in order to detect inter-correlated predictors. However, as all these correlations were well below 0.8 (cf. Denoël and Ficetola 2008), all the environmental variables were employed in the model.

Figure 3. A) Male great crested newt. B) Male smooth newt. C) Preparing article **III** bydigging fences. D) A fence in operation.

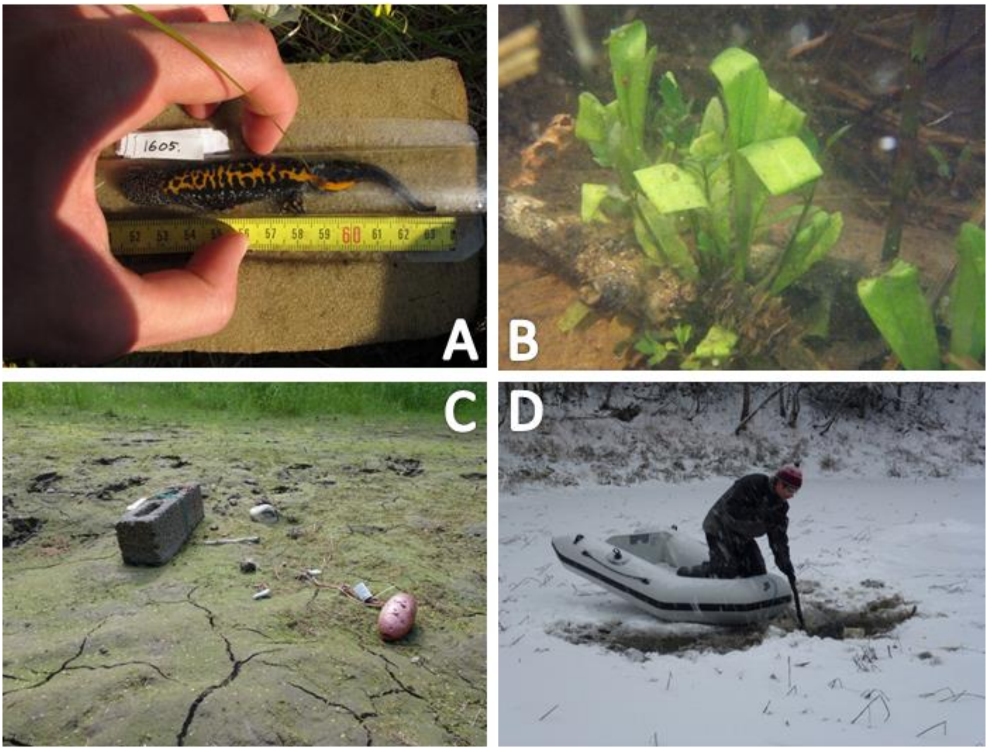

Figure 4. A) Captured newts in article **III** were photographed for later identification. B) Eggs laid on *Myosotis laxa*. C) Water height and temperature loggers at the bottom of a dried pond. Note the bear bites on the float. D) A somewhat late fetch of loggers.

Examination of residuals from the first model runs indicated that three ponds appeared to be statistical outliers in the analysis (see Lehmann et al. 2003), and thus they were excluded from the final model building. The GAMs were generated in three main phases. First, a GAM with related newt abundance to the five habitat factors and the area of ponds was developed by using the stepwise procedure outlined above. Second, after developing this first GAM, the most reasonable ecological interaction variables were created based on species ecology by multiplying 1) herb-rich forest by the number of ponds and 2) unsuitable habitats by the number of young stands (cf. Crawley 2007). These two interactions were then entered in the first GAM one at a time, and the difference in the goodness of fit of the models with and without the interaction terms were tested using ANOVA. In the third step, GAMs with only pond area, or number of ponds in the neighborhood, or both, were modeled. Finally, the performance of these GAMs and the first GAM were compared and tested with ANOVA (Crawley 2007).

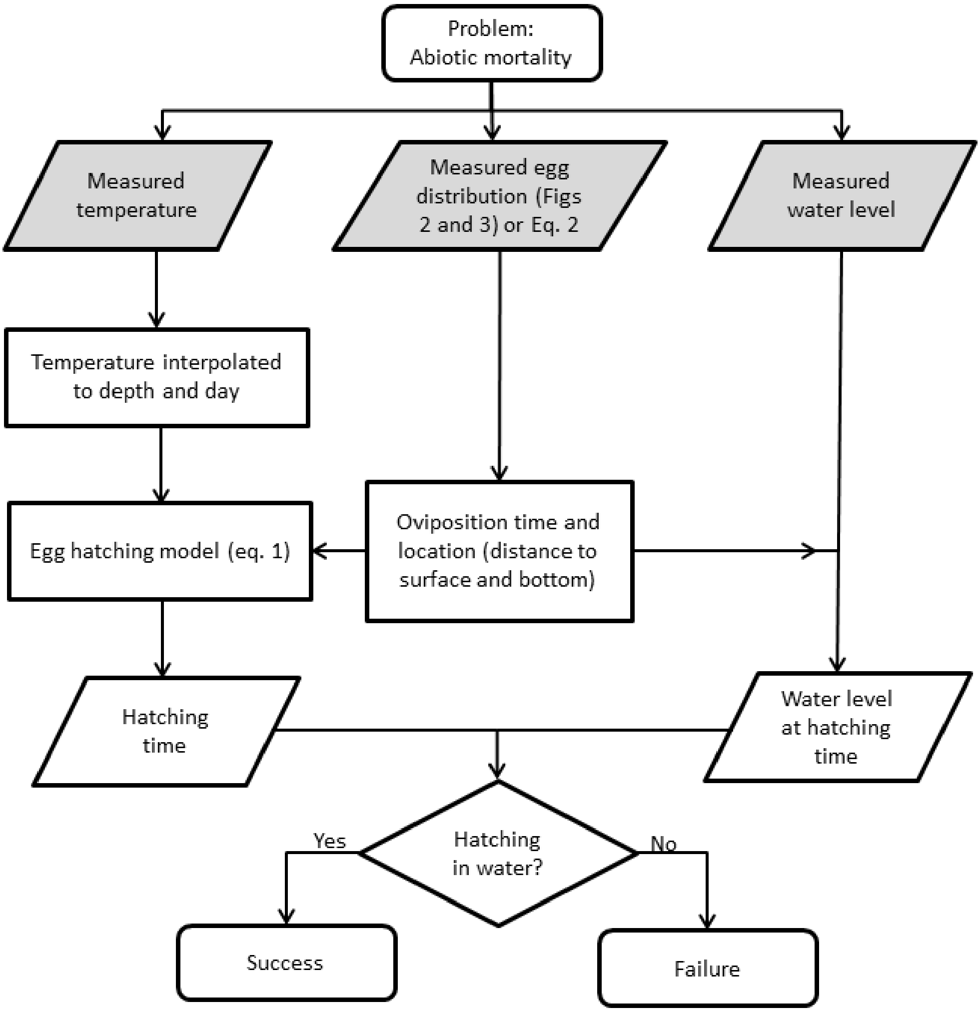

Figure 5. Flow chart of deduction used in article **I**.

2.3.3 Terrestrial habitat use, III

I tested the importance of different environmental properties and their interactions for the total number of captured newts and also for both newt species separately. Adults and juveniles of both species were pooled. The data consisted of counts, which had a Poisson distribution under independence. I fitted all models using a Poisson generalized linear mixed model (GLMM). Using logarithmic fence length as a predictor in the model implies that the coefficients give the relative effect to the newts per meter of fence. The model predictions can therefore be interpreted as relative estimates of newt individuals. In the initial model, zone, fertility, age, year, and logarithmic length of the fence together with all first-order interactions of categorical predictors were fitted as fixed effects, with a random constant at the nested levels of individual fences, compartments, and ponds. The final model was selected by removing variables or interactions of variables with the highest *p*-value one at a time, so that at the end only statistically significant variables remained. The pond-level variance was 0 and therefore the final model included a random constant only at the nested levels of individual fences and compartments. Therefore, the final model for the number of captures in year *t* for fence *i* in stand *j* around pond *k* was:

$$y_{kjit} = Poisson(\lambda_{kijt}), \qquad \text{(Eq. 2)}$$

where the expected value can be written as

$$\lambda_{kij} = \exp(\beta' x_{kijt} + b_{ki} + b_{kij}). \qquad \text{(Eq. 3)}$$

The term $\boldsymbol{\beta}'\boldsymbol{x}_{kijt}$ includes the effects of fixed predictors and the random effects b_{ki} and b_{kij} have a normal distribution with a mean of 0 and unknown variances. Analyses were conducted using the statistical software package SPSS version 19.0 (IBM SPSS Statistics for Windows. Armonk, NY, USA).

2.3.4 Connectivity, IV

Stand ages in the future landscape scenarios were calculated using the reclass tool of the Spatial Analyst package of ArcGIS 10.1 software. At the start, stand ages were classified at ten-year intervals. Next, I selected those stands (pixels) were ready for harvest (i.e. at 60 or 80years). In the following 10-year period, cut stands were assigned an age value of 0 year; for other stands, ten years were added to their age. This stepwise reclassification was repeated ten times (from 2011 to 2111).

In the modeling, I concentrated on the general breeding potential of each pond, rather than on estimates of the numbers of larvae, juveniles or adults as they show large annual variations. Using the presence of fish (*Fi*), pH-value (*pH*), breeding success (*Br*) and the probability that a pond would dry out (*Dr*) (see article IV for details), I calculated the extinction value *E* for a pond with the following formula:

$$E = 1- (Fi*pH*(Br+Dr))/6 \qquad \text{(Eq. 4)}$$

If either fish or *pH* variables had the value of zero, the pond was not suitable for breeding, i.e. the extinction coefficient is 1. If both fish and *pH* variables have a value of 1, then the value of extinction is defined by the sum of the breeding success and the probability of drying. The result of the formula was scaled to be between zero and one. The closer the result of the formula was to one, the greater was the extinction probability in a given pond.

The immigration potential (*Im*) of each pond was calculated in several steps. First, I estimated the descendant production potential for each pond using previously defined parameters:

$$Fi * pH * (Br + Dr) \qquad \text{(Eq. 5)}$$

The next step was to sum this descendant production potential within a 1 km radius of each pond. Immigration potential measures the isolation of a pond by also taking into account the number of ponds and their breeding success within the dispersal distance.

Connectivity (*Co*) of the landscape was calculated by compiling a spatial data layer where shelter-providing areas (forests and forested peatlands) were assigned a value of 1 (suitable for dispersal), while open areas, clear-cuts and fields, together with water bodies with fish were assigned a value of 0 (not suitable for dispersal). Thereafter, I calculated the proportion of areas suitable for dispersal within a 1 km radius of each pond. The selected 1 km dispersal distance is a widely used threshold for the great crested newt or related species dispersal (Kupfer and Kneitz 2000, Oldham et al. 2000, Trenham et al. 2003, Van Buskirk 2005).

The colonization C for each pond is the average value of the two parameters:

$$C = (Im + Co)/2 \qquad \text{(Eq. 6)}$$

I also calculated the probability of successful breeding using the incidence of occupancy (J_p) (Hanski 1994) for each pond (p) with the above mentioned values of extinction (E_p) and colonization (C_p):

$$J_p = C_p / (C_p + E_p) \qquad \text{(Eq. 7)}$$

In order to examine the population dynamics of the great crested newt in a regional pond network, I used E and C values as probability estimates that ponds would become extinct or colonized. If a pond was unpopulated, it was colonized again with the probability of C_p. If a pond was a current breeding pond, the larvae population was prone to become extinct with the probability of E_p. Extinction and colonization events were decided by drawing a random number between zero and one from a uniform probability distribution. This random number was then compared with E_p or C_p. The extinction or colonization of ponds was recalculated for each pond using 20 time steps. The length of a time step was set at one year. This 20-year-long projection was replicated 50 times while keeping the landscape characteristics unchanged to determine the variation in pond occupancy. Population projections were modeled for all four landscape scenarios to study how population persistence depended on the regional landscape structure.

Computer simulations were carried out with SELES (spatially explicit landscape event simulator) software. SELES is a domain-specific computer language for modeling landscape dynamics (Fall and Fall 2001).

3 RESULTS

3.1 Oviposition, I

I found the first newt eggs on May 18, 2014, six days after the arrival of the newts in the pond. The egg laying period lasted approximately one month. Most of the eggs (84 %) were laid on the dead leaves of grasses and sedges. Living plants were used as an oviposition substrate as soon as they emerged in late May. On June 2 and 9, 43 % and 63 % of the eggs respectively were laid on living plants.

The newts clearly favored the surface of the pond for oviposition, with 72 % of eggs found in the 0-19 cm (from the water surface) depth. Although very shallow sites (0-9 cm from the bottom of the pond) were seldom used for oviposition, four eggs of the total 614 were found from this depth.

The effect of cumulative heat summation (temperature above 5°C at 10 cm depth) on oviposition followed a sigmoidal curve (R^2=0.907, $p < 0.001$):

$$y = \frac{a}{1+\left(\frac{x}{x_0}\right)^b} \qquad \text{(Eq. 8)}$$

I found that early oviposition produced the best estimated hatching results. This success rate stayed high for a couple of weeks and then dropped dramatically in three out four ponds. One of the study ponds showed a clearly different pattern due to exceptionally low water levels after snow melt.

3.2 Breeding success, II

The final GAM explained 58 % of the total deviance in variation in newt breeding success. The correlation between the observed and fitted larval newt abundance values was notably high in the simple validation (r = 0.762, see Lehmann et al. 2003), but somewhat lower in the four-fold cross validation results (r = 0.652). The main factor that explained breeding success was the area of herb rich forests. Subordinate contributions were related to the area of unsuitable habitats and shade (model contributions), and the highest proportion of broadleaved trees in a forest stand (single contribution).

The relationship between the area of herb rich forests and breeding success showed a positive correlation from one hectare upwards, and the ponds with the highest breeding success were also correlated with the highest proportion of broadleaved trees in a forest stand. In contrast, lower breeding success was associated with increases in shade, area of young forest stands and area of unsuitable habitats in the vicinity of the ponds.

GAMs that included only the pond area, or the number of ponds within a radius of 500 m, or both, explained only a very modest amount of the variation in newt breeding success (the percentage of explained deviance D^2 = 6.63, 8.31 and 14.16, respectively). Consequently, the final GAM with five habitat variables had a significantly better performance than the three GAMs with spatial variables ($F_{-4.04}$ = 10.566, p = 0.000096, $F_{-4.04}$ = 10.220, p = 0.00013, $F_{-1.04}$ = 39.94, p = 0.0000075, respectively).

3.3 Terrestrial habitat use, III

I clearly found fewer newts from forests that were located far from the ponds. The captures of both species in the 0–25 m distance zone differed from those in the 25–50 and 50–75 m zones. Understory vegetation cover was related to the occurrence of the newts. On average, almost three times more individuals were captured from the high-cover sites in comparison to sites with the lowest vegetation cover (*mean* ± *SE*: 0.93 ± 0.154 and 0.32 ± 0.075, respectively; $p = 0.003$). The difference in capture rates for the two newt species was apparent in low vegetation cover sites; those sites were clearly avoided by great crested newts but not by smooth newts, which were found three times more frequently than great crested newts in those sites (interaction for species x understory cover, $p = 0.001$).

Although I did not capture great crested newts in the clear-cut areas, the number of captures peaked in young sites, in contrast to smooth newts, which avoided young sites. Significant ($p < 0.05$) differences in the capture rates of great crested newts were found between the youngest and oldest sites, while smooth newt captures differed between young sites and sites of intermediate age class ($p < 0.05$). Interspecific differences were found in intermediate and old age classes ($p < 0.01$,) but not in the youngest sites ($p = 0.058$). This pattern was also valid for all three distance classes, i.e. the rare species preferred young forests and the common species older forests regardless of the distance of the forest from the pond. Smooth newts did not show any difference in capture rates between clear-cut areas (1.00 ± 0.356) and all the other sites (1.15 ± 0.136; Mann-Whitney U-test: n, df, $p = 0.584$).However, in the case of the smooth newt, the division of the data into different distance classes revealed more details of their general habitat use. As noted earlier, captures of the smooth newt peaked slightly at intermediate aged sites, but this pattern was only verified from zone one, (i.e. 0 – 25 m).

Newt species captures differed markedly between the age classes with a different understory cover. The main difference between the species was in the middle-aged and older stands with a low understory cover; those sites were strongly avoided by great crested newts but not by smooth newts. In the intermediate aged and older forests, great crested newts occurred almost exclusively on sites where the understorey cover was high ($p < 0.01$). Within the lowest cover class (< 46 % cover), more great crested newt captures were recorded in the youngest sites compared with the intermediate and older sites ($p = 0.007$ and $p = 0.004$, respectively).

Smooth newts were captured most frequently from the old forest sites with high ground cover vegetation (> 63 % cover). Captures from these favored sites were significantly different from older sites with low ground cover ($p = 0.012$) and from the younger sites with high ground cover ($p = 0.024$). Among the youngest sites, intermediate ground cover had lower capture rates compared to low ($p = 0.019$) and high ground cover classes ($p = 0.037$). In the intermediate ground cover class the amount of captured smooth newts increased significantly from the youngest to medium-aged sites ($p = 0.004$).

In the youngest sites, great crested newts clearly favored sites with high shelter-providing vegetation compared to smooth newts ($p = 0.006$). In medium-aged sites with low ground cover vegetation, smooth newts outnumbered great crested newts ($p = 0.018$). Within the oldest sites, more of both species were captured when ground cover increased from the lowest to the highest level.

3.4 Connectivity, IV

The change from the historic to the current landscape was noticeable as the number of ponds with the lowest incidence of occupancy more than tripled from 41 to 127, while the number of ponds with a high incidence of occupancy was reduced by approximately 50%. The number of ponds with the lowest incidence of occupancy continued to increase under both future landscape scenarios, although the numbers were only slightly greater in the shorter 60-year logging rotation scenario as compared with the 80-year logging rotation scenario. Following the sharp past–present drop in the number of ponds with the highest incidence of occupancy, numbers remained constant under the future landscape scenarios.

Prior to the start of intensive human activities, 94 % of the ponds had a incidence of occupancy value greater than the “worst” presently observed breeding pond (0.4). In the current and future landscapes, the proportion of ponds above this threshold varied between 50–52 %. In contrast, the future scenarios with different logging rotations had only minor effects on the pattern of incidence values of the ponds.

Average extinction probabilities (at pond level) decreased fundamentally with increasing incidence category in all landscapes. The difference in extinction probability between the highest and lowest incidence categories was about six-fold in the past, but increased to 20–

22-fold in the current and future landscape scenarios. There was more variation in the extinction values than in the colonization values among the different categories.

Ponds were divided based on their extinction and colonization probabilities. The difference in proportion of the worst ponds (low *C*, high *E*) was more than six-fold between the historic and future B landscapes while the proportion of best ponds (high *C*, low *E*) in the future B landscape was 50 % lower than in the historic landscape.

The ponds were classified into three groups based on the mean number of ponds that stayed colonized (i.e. successful breeding) in the 20 time steps (years): >10 consecutive successful breedings, 1-10 consecutive successful breedings and <1 consecutive successful breeding. The proportion of ponds where the modeled reproduction of newts was successful in more than 10 successive time steps dropped from 25% in the historic landscape to 11 and 10% in the current and future landscapes respectively. The proportion of ponds where reproduction failed repeatedly increased from 8 % in the historic landscape to 51 % in the current and future landscapes.

4 DISCUSSION

4.1 Oviposition, I

Ephemeral ponds show high inter-annual variability in duration, frequency, depth, temperature and timing of seasonal flooding (Pyke 2004). Study I has shown that the variability of the pond hydrological system seriously hampered the habitat quality for the newts. One of the study ponds has frequently been shown to have one of best breeding success rates in Eastern Finland (V. Vuorio et al., unpublished data). However, as a result of the exceptionally low snow cover in the previous winter of this study, the pond did not receive the normal amount of melt water and the pond was completely dried up by mid-July resulting in total larvae mortality.

Hydroperiod has been earlier identified as a critical element in amphibian species richness, productivity and successful metamorphosis in natural amphibian populations (Semlitsch and Wilbur 1988, Pechmann et al. 1989, Snodgrass et al. 2000, Paton and Crouch 2002). In addition to hydroperiod *per se*, I documented the importance of hydrodynamics during the egg period. Since eggs are unable to travel, it is critical that water remains present at the oviposition site until hatching has taken place. In this respect, a sufficient water depth at the oviposition site to keep eggs submerged is the most important factor for the egg survival.

I found that the importance of abiotic factors increased the later the egg was laid. Early season eggs showed the best survival rates. This success is determined by climatic factors, temperature and water level, which in turn are regulated by rainfall, amount of snow, permeability of the bottom of the pond and the water storage in the surroundings (Leibowitz and Brooks 2008).

Early season breeders showed the best success rate, but their arrival to ponds is limited by the rains and temperature (Verrell and Halliday 1985, Semlitsch et al. 1993, Griffiths 1997, Murton 2009). At the beginning of the field season some of our ponds were almost completely free from ice, but no newts were present. They started to arrive around mid-May, following the first rains.

The results of this study suggest that newts are adept at optimizing oviposition site selection to minimize the risk of desiccation. There were only a very small number of eggs found in shallow water areas. In addition, newts stopped breeding much earlier in the pond that had a significant drop in the water level.

The resource use of large- and small-bodied newts is significantly different (Jehle et al. 2000). A replication of study **I** is needed so that species can be separated to better determine interspecific differences. In practice, one solution would be to cut the piece of the leaf with the laid egg and to store it in the same pond under the water in a small numbered container that has good ventilation. After hatching, identification of the species would be easy and the individual could then be released into the same pond. This would give additional information at the species level in regard to hatching rate, preferences concerning timing, depth, oviposition, plant species and exposition.

4.2 Breeding success, II

Herb-rich forests (coniferous or mixed) in the surroundings of a pond were the habitat features that best explained breeding success. In effect, herb-rich forests provide hiding places from predators, shelter from desiccation and an abundance of nutrition for great crested newts (Jehle and Arntzen 2000). These factors would seem to improve the survival of individuals in the vicinity of the ponds and result in higher breeding in the ponds, in comparison to ponds that have other types of forest in their surroundings. Interestingly, the proximity of forests have been found to be critical for newt occupancy and the maintenance of larger populations in Central Europe (Denoël and Lehmann 2006, Denoël and Ficetola 2007, 2008). Herb-rich lush forests provide cover for the newt on the shores of their breeding ponds; a general pattern consistent across different biogeographical zones in Europe.

The shape of the response curve suggests there is an ecological threshold in regard to the area of herb rich forests that the newts prefer or need, i.e. approximately 1ha. Below this threshold, the area of suitable terrestrial habitat acts as a limit to the breeding of the great crested newt. Ponds with less than 1 ha of herb rich forest in their close vicinity appear to be sub-optimal environments for the great crested newt.

There was a positive relationship between the high proportion of broadleaved trees in a forest stand and breeding success in the great crested newt. This relationship may be explained by the large amounts of leaf litter provided by the broadleaved deciduous trees, which leads to an increase in the soil pH and in the amount of nutrients and invertebrate prey items on the ground (Wareborn 1992, Ponge 2003), and a subsequent increase in the number of adults and breeding activity. In contrast, breeding success in the young forests was lower.

Unsuitable habitats appeared as the third most important habitat variable in the model. As expected, this compound variable showed a negative relationship with breeding success. Interestingly, the importance of this effect only became apparent after the additive stacking of all unsuitable habitats; individually they did not show any statistical significance due to the high variability and small surface areas of these habitats.

I investigated how the breeding success of the great crested newt can be explained by the spatial variables commonly used in metapopulation studies, namely the area and isolation of a pond, in comparison to terrestrial habitat factors. The results showed that the pond area and the number of all ponds, with or without the great crested newt, within a radius of 500 m (reflecting the isolation of the pond) are poor predictors of the reproductive success of the great crested newt in our study area. This was particularly evident when the amount of explained deviance was compared. GAMs with pond area, isolation or both explained four to five times less variation in breeding success than the GAM with the five habitat variables. Thus, it appears that pond area or isolation may not be reliable predictors of the best reproductive sites for the great crested newt in forest-dominated boreal landscapes.

In a similar vein, Pellet et al. (2007) found the connectivity of habitat patches had a surprisingly small effect on the colonization extinction dynamics of amphibians. One reason for the absence of area or isolation effects may be that established populations of long lived amphibians are relatively stable as long as the habitat remains largely undisturbed. In such situations, extinction and colonization events do not become apparent within the short time frame of most ecological research. Marsh and Trenham (2001) argued that the isolation effect of a pond may be strongest in areas where the surrounding terrestrial habitats are highly altered. Moreover, they suggested that isolation effects may actually be better explained by the distribution of terrestrial habitat than by the isolation of breeding ponds themselves. The findings of this study are concordant with the conclusions of Pellet et al. (2007) and Marsh and Trenham (2001), and suggest that the study area and corresponding forest-dominated boreal landscapes represent less disturbed environments for amphibians than the densely-populated central and southern European regions.

4.3 Terrestrial habitat use, III

The comparisons between rare and common newt species revealed some clear patterns. It was found that, in the surroundings of the breeding ponds, patch properties had a major influence on the occurrence of both species in a patch. Understory shelter was decisive but forest age also mattered. It was also found that the longer the distance from the breeding pond, the more selective the species became in their habitat choice. The rare species, in particular, always seemed to require understory vegetation shelter although not necessarily old forest.

Shelter-providing vegetation provides protection against water loss and thermal stress (Mazerolle and Desrochers 2005). The importance of ground cover was clearly visible within all the distance classes separately, and by the fact that no great crested newts were captured from treeless clear-cut areas. The combination of age and ground cover together revealed essential interactions; the greatest difference in newt captures was found in old forests between low and high vegetation cover. This suggests that the age or canopy cover of the forest alone is not an adequate factor to determine the quality of the terrestrial habitat of newts. More important is the cover of vegetation that provides direct shelter on the forest floor. Newts have been found to use ground-covering objects, such as grass tussocks, logs, or burrows as land refuges. Newts return to these refuges during the day after nightly movements or use the refuges for aestivation and overwintering (Jehle 2000, Jehle and Arntzen 2000, Schabetsberger et al. 2004, Malmgren et al. 2007).

At the start of the study, I anticipated that newts would avoid recently clear-cut areas and would be found in increased numbers along a forest chronosequence, with numbers peaking among the oldest forests. As expected, clear-cuts were devoid of great crested newts in this study, although a somewhat surprising decreasing trend in great crested newt captures was observed with increasing age of the forest, while smooth newts clearly favoured intermediate and older sites. However, smooth newts did not show any difference in captures in clear-cuttings compared with all the other sites.

The results of this study showed that within ten years of clear-cutting the sites were already used frequently by the newts. Ash (1997) found that salamanders returned to clear-cut areas after 4–6 years following rapid growth of understory vegetation, which creates favorable microclimatic conditions on the forest floor (Brooks and Kyker-Snowman 2008). In spite of the relatively low canopy covers, these young sites probably have a sufficient ground layer to provide shelter to newts (for cover data, see Lakka and Kouki (2009)).

The distance of the habitat from the pond had a major effect on newt abundance. The number of captures in the vicinity of the ponds was more than double compared with captures 50–75 m away from the shoreline. Since the terrestrial habitats around the ponds are often inhabited by the newts and since they have a clear preference for specific habitats, our results support the concept of maintaining buffer zones around the breeding ponds. The highest numbers of smooth newts were found in old forests, with a dense field layer vegetation of herbs and grasses. These conditions are best met if forests are not intensively managed and, in particular, if clear-cuttings are avoided. However, the maintenance of a herbaceous field layer may require the creation of small-scale gaps in the canopy to avoid an overly dense canopy cover that is typical for even aged monoculture forests.

In general, the understory vegetation is influenced by the dominant tree canopy cover composition and structure via modifications of resource availability such as light, water, and soil nutrients together with the physical characteristics of the litter layer (Barbier et al. 2008). Single-tree selection has been shown to maintain mixed multi-storied stands with more diverse understory vegetation (Smith et al. 2008, Zenner et al. 2011, Duguid and Ashton 2013). Instead of planting spruce monocultures in the vicinity of the breeding ponds, consideration of the use of single-tree selection as a forest-harvesting method may be worthwhile to improve the quality of the terrestrial habitats.

In addition to habitat type, the width of the buffer zone is highly important. This zone should extend far enough to include all habitats at different life stages (Semlitsch and Bodie 2003). The interaction of distance and understory cover showed that the occurrence patterns of great crested newts were not similar in all zones. To facilitate movement of the newts, clear-cuts should not be applied within the buffer zones. Furthermore, soil scarification is likely to be extremely harmful for the great crested newts as it destroys the protective ground vegetation.

The effect of forest management in terms of canopy age was contrary to initial predictions. The common species avoided the young age classes created by loggings while the rare one favoured them. The reasons for this difference in behavior patterns cannot be directly deduced from the data and was somewhat unexpected. Differences in food resources, humidity, or avoidance of the same habitats by the smooth newts in the presence of great crested newts might lie behind the pattern. However, factors other than canopy age probably determine the terrestrial habitat use of great crested newts.

4.4 Connectivity, IV

Metapopulation studies have traditionally emphasized the importance of connectivity (Hanski and Ovaskainen 2000, Eycott et al. 2012, Van Buskirk 2012). However, habitat loss and degradation seem to be more important factors for the great crested newt (see also Nystrom et al. 2007). The increasing intensity of forestry and the introduction of fish into the ponds strongly decreased the incidence of occupancy, i.e. how often the species can breed successfully in a pond. The reason for the trend is the dramatic decrease in the “reproductive capacity” of ponds (i.e. increase in extinction E in the model).

The studied species probably faced the greatest habitat loss when modern forestry was introduced in the mid 20th century. This change very likely decreased connectivity via habitat deterioration. Fish introduction via the drainage networks destroyed the breeding ponds and, thus, increased extinction rates in the modelled landscapes. Amphibians have been shown to be sensitive to habitat alteration, (Ficetola and De Bernardi 2004) and to the introduction of fish (Joly et al. 2001, Skei et al. 2006, Hartel et al. 2007). Hecnar and McLoskey (1996) presume that amphibian declines largely originate from reduced opportunities for colonization together with the increased frequency of extinction.

Habitat degradation with increased *E* appeared to be the key factor that affected the amphibian population network in the landscape. However, extinction and colonization are linked; an increase in *E* has severe consequences on the colonization potential of the metapopulation. Decline and extinctions of amphibian populations largely result from the low recruitment of dispersing individuals (Vos and Chardon 1998, Bulger et al. 2003). The loss of suitable breeding ponds has apparently led to a sparser current pond network, thus, blocking the recruitment of ponds, which had a negative effect on breeding pond distribution at the landscape level.

Future landscape scenarios suggest only relatively minor changes in landscape quality compared with the current state of the study region. However, the predicted change between the current and future scenarios emphasized the importance of habitat connectivity. The lowest landscape-level incidence was in the most disturbed landscape, i.e. in the future 60-year logging rotation scenario, which resulted in a decrease in colonization. The reason for the notable decrease in the quality of the landscape was found to be due to the increase in the number of ponds in the lowest incidence category associated with increasing forest use intensity.

5 CONCLUSIONS AND FINAL REMARKS

5.1 Oviposition, I

The biggest future threat is likely to be climate change. In southern Finland the number of days with snow cover together with the snow water equivalent are expected to decrease significantly in the future (Jylha et al. 2008, Jylhä et al. 2009, Raisanen and Eklund 2012). Climatic conditions are predicted to have dramatic effects on ephemeral pond hydrology (Brooks 2004, Leibowitz and Brooks 2008, Brooks 2009, Hartel et al. 2011). More studies though, are needed to enhance our understanding regarding the response of boreal ephemeral ponds and their biota to climate change. The model used for the effect of cumulative heat summation for oviposition in article **I** has been developed for this purpose. The water balance of the breeding ponds should be studied and modeled in detail in order to be able to define which populations face the greatest risk due to the temporal variation of the hydroperiod.

5.2 Breeding success, II

Gustafson et al. (2011) concluded that the occurrence patterns of the great crested newt may be predicted by the terrestrial habitat characteristics of the surrounding landscape. I agree with this conclusion. In article II it is shown that the reproductive success of the newt species is intimately related to habitat factors, in particular the abundance of herb-rich forests and deciduous trees. This is an important finding, because presence-absence occurrence data do not necessarily predict the viability of a population in a patch, whereas from an ecological perspective the abundance of juvenile newts and the underlying environmental drivers may provide a useful basis for the separation of stable populations from ones in decline, and for the prediction of suitable locations for as yet undiscovered viable newt populations.

5.3 Terrestrial habitat use, III

Article III showed that the combination of tall trees and dense understory cover forms the most attractive habitat for the newts in the forested landscape. Thus, to facilitate movement in terrestrial habitats, the maintenance of protective vegetation around the breeding ponds is essential. If natural canopy openings are rare due to planted monocultures, small-scale habitat restoration or selective cuttings may be needed to maintain a diverse herbaceous layer that provides ground-level shelter.

It was also found that there are notable differences between the two newt species. It appeared that the rare species – the great crested newt – seemed to be less tolerant to changes in sheltering vegetation. At long distances from the breeding ponds, the species almost exclusively occurred on sheltered sites only, whereas the smooth newt was still quite common in exposed habitats. This observation suggests that facilitation of the dispersal of the rare species requires that careful attention be paid to forest structure between ponds. It is quite likely that species cannot disperse over long distances if sheltering vegetation is absent. Although fixed-width buffers are administratively simple to implement and monitor, my results suggest that site-specific consideration of buffer width would benefit the newts, particularly when highly suitable habitats from areas further afield are also included.

5.4 Connectivity, IV

The importance of landscape configuration was shown to be of great importance in the future scenario with the shortened logging rotation. The results from article IV are in line with Marsh and Trenham (2001) who observed that pond isolation had more importance in disturbed environments. This might be explained by the distribution of terrestrial habitats, rather than by the distribution of suitable breeding ponds. If the human impact on the environment is increased, the importance of habitat configuration becomes more important, thus underlining the importance of landscape-level conservation planning. However, the disturbance in the study areas has a temporal dimension. Disturbance is not permanent destruction in this case. Forests are logged, but will regenerate and are accepted as dispersal routes within ten years. This in turn emphasizes the importance of stable breeding ponds and the distance between them.

Knowledge in regard to long-distance dispersal of the great crested newt is unfortunately limited, and the dispersal ability of amphibians is generally underestimated (Smith and Green 2005). It is also possible that the impact of isolation has not been fully quantified (for extinction debt, see Tilman et al. 1994) due to relatively recent land use changes by drainage of mires for forestry purposes, which has destroyed breeding habitats by desiccation, overgrowing and fish dispersion. The great crested newt has only faced these land use threats in the last 50 years, and therefore has a relatively short history of rarity. Such species are expected to have a greater risk of extinction, compared to species with a longer history of rarity (Gaston and Kunin 1997).

5.5 Conservation

My main aim was to provide new and useful information to be able protect the endangered great crested newt efficiently. All the life stages from egg to adult, in both aquatic and terrestrial habitats have been covered in this study. Based on my results and observations, it is possible to define favorable sites for the restoration of old or the excavation of new ponds, delineate the borders of conservation areas and buffer zones.

Based on the results here, the construction of new artificial ponds can be targeted at the most promising sites, where the water level should stay relatively stable during spring time to prevent desiccation of the eggs. Artificial ponds have been found to be an effective method to mitigate the negative impacts of human activity upon many amphibian species, including the great crested newt (Rannap et al. 2009). My results corroborate earlier recommendations to coordinate the management planning of both aquatic and terrestrial habitats when targeting successful conservation of amphibian species (Denoël and Lehmann 2006, Gustafson et al. 2011). For the great crested newt in boreal forests, this means that the conservation of the breeding ponds is not sufficient alone, but that forestry practices in the vicinity of the ponds also need to be adjusted so that the species and its habitat are maintained. In practice this means that herb-rich forests in the vicinity of the ponds should be preserved and deciduous trees should be favored in other forest types, so that forest management should not result in open, sunny forest floors with a loss of food resources and hiding places for the great crested newt.

This study has also shown that tall trees, together with a high understory cover form the most attractive habitat structure for the newts in the forested landscape. Thus, the maintenance of protective vegetation around the breeding ponds is essential to facilitate movement in terrestrial habitats. If natural canopy openings are rare due to planted monocultures, small-scale habitat restoration or selective cuttings may be needed to maintain a diverse herbaceous layer that provides ground-level shelter.

The results also showed that the rare species – the great crested newt – seemed to be less tolerant to changes in sheltering vegetation. At long distances from the breeding ponds, the species almost exclusively occurred on sheltered sites only, whereas the smooth newt was still quite common in exposed habitats. This observation suggests that facilitation of the dispersal of the rare species requires careful attention in order to maintain suitable forest structure between ponds. It is quite likely that species cannot disperse over long distances if sheltering vegetation is absent.

Wiens (2006) suggested that the conservation of a habitat area is important; if a habitat is not yet fragmented. If a habitat is highly fragmented due to land use, one should also focus on restoration of the habitat area because a small increase in quality and quantity can make a difference. Between these two extremes, it is highly important to reduce the deleterious effects of fragmentation by focusing on the habitat connectivity in the landscape matrix (Wiens 2006). For amphibians, the matrix also has a high conservation value since it is the main habitat for dispersing juveniles and for adults navigating to their hibernation sites.

Forest management that favors short rotation times may cause an additional threat to the persistence of great crested newt populations, particularly if it leads to more disrupted dispersal routes, thus increasingly the isolation of the suitable breeding ponds from one another. In effective landscape management, the limited resources should be invested wisely in order to gain the greatest biodiversity return. Conservation efforts must be targeted in securing the core areas. Therefore, all forestry actions that potentially increase the extinction risk (E) must be considered carefully. It is evident that fish should not be allowed to colonize fishless ponds via new ditches or introductions (Joly et al. 2001, Skei et al. 2006, Hartel et al. 2007). The water quality of the ponds should not decrease due to logging or ditching activities. Furthermore, logging in the vicinity of breeding and potential breeding ponds should be avoided or completed using selective cutting (Halley et al. 1996, Vuorio et al. 2015). The canopy layer and understory vegetation must not be disturbed since it should offer enough shelter for the newts against predators and from desiccation (Halley et al. 1996, Jehle and Arntzen 2000, Gustafson et al. 2009, Vuorio et al. 2013, Vuorio et al. 2015).

Actions that increase the colonization probability (C) must be actively encouraged. Above all, connectivity between the core area ponds and the prevailing good quality ponds should be ensured. Increasing connectivity, *per se*, might not always be justified. For example, an increased connectivity between two low quality ponds with a high E may be a low priority. Thus, increasing the connectivity between high quality habitats should be set as a target.

Can the great crested newt survive in managed forest landscapes? The answer is yes, as long as the status of breeding ponds has not deteriorated, there are sufficiently wide buffer zones left around the breeding ponds, forest practices are modified in the inter-pond matrix so that the canopy cover remains, and pond restoration and the excavation of new ponds at carefully selected sites are prioritized.

REFERENCES

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

AmphibiaWeb (2014). Information on amphibian biology and conservation, *Lissotriton vulgaris*. http://amphibiaweb.org. [Cited 16 September 2014].

Arntzen J.W., Kuzmin S., Beebee T., Papenfuss T., Sparreboom M., Ugurtas I.H., Anderson S., Anthony B., Andreone F., Tarkhnishvili D., Ishchenko V., Ananjeva N., Orlov N., Tuniyev B. (2009a). *Lissotriton vulgaris* IUCN Red List of Threatened Species. Version 2012.2. www.iucnredlist.org. [Cited 6 June 2013].

Arntzen J.W., Kuzmin S., Jehle R., Beebee T., Tarkhnishvili D., Ishchenko V., Ananjeva N., Orlov N., Tuniyev B., Denoël M., Nyström P., Anthony B., Schmidt B., Ogrodowczyk A. (2009b). *Triturus cristatus.* IUCN Red List of Threatened Species. Version 2012.2. www.iucnredlist.org. [Cited 20 April 2014].

Ash A.N. (1997). Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conservation Biology 11: 983-989. http://dx.doi.org/10.1046/j.1523-1739.1997.96172.x

Austin M.P. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157: 101-118. http://dx.doi.org/10.1016/s0304-3800(02)00205-3

Barbier S., Gosselin F., Balandier P. (2008). Influence of tree species on understory vegetation diversity and mechanisms involved - A critical review for temperate and boreal forests. Forest Ecology and Management 254: 1-15. http://dx.doi.org/10.1016/j.foreco.2007.09.038

Beebee T.J.C., Griffiths R.A. (2005). The amphibian decline crisis: A watershed for conservation biology? Biological Conservation 125:271-285. http://dx.doi.org/10.1016/j.biocon.2005.04.009

Belgian Species List (2015). *Triturus cristatus* Laurenti, 1768. http://www.especes.be/en/2380. [Cited 26 May 2015].

Björn I. (1991). Suur-Ilomantsin historia. Enon, Ilomantsin ja Tuupovaaran historia vuoteen 1860. Enon, Ilomantsin ja Tuupovaaran paikallishistoriatoimikunta. ISBN 952-90-2104-6. 809 p.

Bol L. (2007). Massachusetts Forestry Conservation Management Practices for MESA-listed mole salamanders, version 2007.1. Westborough, Massachusetts, USA. 31 p.

Briggs L., Rannap R., Pappel P., Bibelriether F., Päivärinta A. (2006). Monitoring methods for the great crested newt *Triturus cristatus*. In: Protection of the great crested newt.

Best practice guidelines. Ministry of the Environment of the Republic of Estonia. ISBN 978-9985-881-69-9. p. 73-84.

Brooks R.T. (2004). Weather-related effects on woodland vernal pool hydrology and hydroperiod. Wetlands 24: 104-114. http://dx.doi.org/10.1672/0277-5212(2004)024[0104:weowvp]2.0.co;2

Brooks R.T. (2009). Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. Climatic Change 95: 469-483. http://dx.doi.org/10.1007/s10584-008-9531-9

Brooks R.T., Kyker-Snowman T.D. (2008). Forest floor temperature and relative humidity following timber harvesting in southern New England, USA. Forest Ecology and Management 254: 65-73. http://dx.doi.org/10.1016/j.foreco.2007.07.028

Bulger J.B., Scott N.J., Seymour R.B. (2003). Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. Biological Conservation 110: 85-95. http://dx.doi.org/10.1016/s0006-3207(02)00179-9

Carr L.W., Fahrig L. (2001). Effect of road traffic on two amphibian species of differing vagility. Conservation Biology 15: 1071-1078. http://dx.doi.org/10.1046/j.1523-1739.2001.0150041071.x

Cogălniceanu D., Rozylowicz L. (2015). Amphibian conservation and decline in Romania. Amphibian Biology 11: 87-98.

Cosentino B.J., Schooley R.L., Phillips C.A. (2011). Connectivity of agroecosystems: dispersal costs can vary among crops. Landscape Ecology 26: 371-379. http://dx.doi.org/10.1007/s10980-010-9563-1

Crawley M.J. (2007). The R Book. John Wiley & Sons, Ltd, Chichester. ISBN-13: 978-0-470-51024-7. 942 p.

Creemers R. (2003). Red list of reptiles & amphibians in the Netherlands. In: Proceedings of an International Seminar in Leiden. Netherlands Commission for International Nature Protection. p. 121-125.

Cvijanovic M., Ivanovic A., Kolarov N.T., Dzukic G., Kalezic M.L. (2009). Early ontogeny shows the same interspecific variation as natural history parameters in the crested newt (*Triturus cristatus* superspecies) (Caudata, Salamandridae). Contributions to Zoology 78: 43-50.

deMaynadier P.G., Hunter M.L. (1998). Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12: 340-352. http://dx.doi.org/10.1046/j.1523-1739.1998.96412.x

Denoël M. (2012). Newt decline in Western Europe: highlights from relative distribution changes within guilds. Biodiversity and Conservation 21: 2887-2898. http://dx.doi.org/10.1007/s10531-012-0343-x

Denoël M., Ficetola G.F. (2007). Landscape-level thresholds and newt conservation. Ecological Applications 17: 302-309. http://dx.doi.org/10.1890/1051-0761(2007)017[0302:ltanc]2.0.co;2

Denoël M., Ficetola G.F. (2008). Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats. Aquatic Conservation-Marine and Freshwater Ecosystems 18: 714-728. http://dx.doi.org/10.1002/aqc.853

Denoël M., Lehmann A. (2006). Multi-scale effect of landscape processes and habitat quality on newt abundance: Implications for conservation. Biological Conservation 130: 495-504. http://dx.doi.org/10.1016/j.biocon.2006.01.009

Denoël M., Perez A., Cornet Y., Ficetola G.F. (2013). Similar local and landscape processes affect both a common and a rare newt species. Plos One 8: 1-11. http://dx.doi.org/10.1371/journal.pone.0062727

Dolmen D. (1988). Coexistence and niche segregation in the newts *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti). Amphibia-Reptilia 9: 365-374.

Dolmen D. (2010). Amfibier og reptiler. In: Kålås, J.A., Viken, Å., Henriksen, S., Skjelseth, S. (eds.) The 2010 Norwegian Red List for Species. Norwegian Biodiversity Information Centre, Norway. p. 413-417.

Duguid M.C., Ashton M.S. (2013). A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. Forest Ecology and Management 303: 81-90. http://dx.doi.org/10.1016/j.foreco.2013.04.009

Edgar P., Bird D.R. (2006). Action plan for the conservation of the crested newt Triturus cristatus species complex in Europe. Council of Europe, Strasbourg. 33 p.

Eigenbrod F., Hecnar S.J., Fahrig L. (2008). Accessible habitat: an improved measure of the effects of habitat loss and roads on wildlife populations. Landscape Ecology 23: 159-168. http://dx.doi.org/10.1007/s10980-007-9174-7

European Commission (2009). Report from the Commission to the Council and the European Parliament. Composite Report on the Conservation Status of Habitat Types and Species as required under Article 17 of the Habitats Directive. COM(2009) 358 final. Brussels. 17 p.

Eycott A.E., Stewart G.B., Buyung-Ali L.M., Bowler D.E., Watts K., Pullin A.S. (2012). A meta-analysis on the impact of different matrix structures on species movement rates. Landscape Ecology 27: 1263-1278. http://dx.doi.org/10.1007/s10980-012-9781-9

Fahrig L. (2007). Non-optimal animal movement in human-altered landscapes. Functional Ecology 21: 1003-1015. http://dx.doi.org/10.1111/j.1365-2435.2007.01326.x

Fahrig L., Pedlar J.H., Pope S.E., Taylor P.D., Wegner J.F. (1995). Effect of road traffic on amphibian density. Biological Conservation 73: 177-182. http://dx.doi.org/10.1016/0006-3207(94)00102-v

Fall A., Fall J. (2001). A domain-specific language for models of landscape dynamics. Ecological Modelling 141: 1-18. http://dx.doi.org/10.1016/s0304-3800(01)00334-9

Ficetola G.F., De Bernardi F. (2004). Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. Biological Conservation 119: 219-230. http://dx.doi.org/10.1016/j.biocon.2003.11.004

Finnish Forest Research Institute (2013). The Multi-source National Forest Inventory Raster Maps of 2011. http://kartta.metla.fi/index-en.html. [Cited 13 August 2013].

Finnish Meteorological Institute (2015). Vuositilastot. http://ilmatieteenlaitos.fi/vuositilastot. [Cited 24 August 2015].

Freidenfelds N.A., Purrenhage J.L., Babbitt K.J. (2011). The effects of clearcuts and forest buffer size on post-breeding emigration of adult wood frogs (*Lithobates sylvaticus*). Forest Ecology and Management 261: 2115-2122. http://dx.doi.org/10.1016/j.foreco.2011.03.005

Gaston K.J., Kunin W.E. 1997. Concluding comments. In: Kunin W.E., Gaston K.J. (eds.) The biology of rarity, causes and consequences of rare-common differences. Chapman & Hall, London. p. 262-272.

Gibbs J.P. (1998). Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management 62: 584-589. http://dx.doi.org/10.2307/3802333

Gollmann G. (2007). Rote Liste der in Österreich gefährdeten Lurche (Amphibia) und Kriechtiere (Reptilia). In: Zulka K.P. (ed.) Rote Listen gefährdeter Tiere Österreichs. Checklisten, Gefährdungsanalysen, Handlungsbedarf. Teil 2: Kriechtiere, Lurche, Fische, Nachtfalter, Weichtiere. p. 37-60.

Gomez-Rodriguez C., Bustamante J., Diaz-Paniagua C., Guisan A. (2012). Integrating detection probabilities in species distribution models of amphibians breeding in

Mediterranean temporary ponds. Diversity and Distributions 18: 260-272. http://dx.doi.org/10.1111/j.1472-4642.2011.00837.x

Gould W.R., Patla D.A., Daley R., Corn P.S., Hossack B.R., Bennetts R., Peterson C.R. (2012). Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the greater Yellowstone ecosystem. Wetlands 32: 379-389. http://dx.doi.org/10.1007/s13157-012-0273-0

Griffiths R.A. (1997). Temporary ponds as amphibian habitats. Aquatic Conservation-Marine and Freshwater Ecosystems 7: 119-126.

Griffiths R.A., Dewijer P. (1994). Differential effects of pH and temperature on embryonic development in British newts (*Triturus*). Journal of Zoology 234: 613-622.

Griffiths R.A., Mylotte V.J. (1987). Microhabitat selection and feeding relations of smooth and warty newts, *Triturus vulgaris* and *T. cristatus*, at an upland pond in Mid-Wales. Holarctic Ecology 10: 1-7.

Guerry A.D., Hunter M.L. (2002). Amphibian distributions in a landscape of forests and agriculture: An examination of landscape composition and configuration. Conservation Biology 16: 745-754. http://dx.doi.org/10.1046/j.1523-1739.2002.00557.x

Gulve P.S. (1994). Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75: 1357-1367. http://dx.doi.org/10.2307/1937460

Gustafson D.H., Andersen A.S.L., Mikusinski G., Malmgren J.C. (2009). Pond quality determinants of occurrence patterns of great crested newts (*Triturus cristatus*). Journal of Herpetology 43: 300-310.

Gustafson D.H., Malmgren J.C., Mikusinski G. (2011). Terrestrial habitat predicts use of aquatic habitat for breeding purposes - a study on the great crested newt (*Triturus cristatus*). Annales Zoologici Fennici 48: 295-307.

Gustafson D.H., Pettersson C.J., Malmgren J.C. (2006). Great crested newts (*Triturus cristatus*) as indicators of aquatic plant diversity. Herpetological Journal 16: 347-352.

Halley J.M., Oldham R.S., Arntzen J.W. (1996). Predicting the persistence of amphibian populations with the help of a spatial model. Journal of Applied Ecology 33: 455-470. http://dx.doi.org/10.2307/2404977

Hanski I. (1994). A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151-162. http://dx.doi.org/10.2307/5591

Hanski I., Ovaskainen O. (2000). The metapopulation capacity of a fragmented landscape. Nature 404: 755-758.
http://dx.doi.org/10.1038/35008063

Hartel T., Bancila R., Cogalniceanu D. (2011). Spatial and temporal variability of aquatic habitat use by amphibians in a hydrologically modified landscape. Freshwater Biology 56: 2288-2298.
http://dx.doi.org/10.1111/j.1365-2427.2011.02655.x

Hartel T., Nemes S., Cogalniceanu D., Ollerer K., Schweiger O., Moga C.I., Demeter L. (2007). The effect of fish and aquatic habitat complexity on amphibians. Hydrobiologia 583: 173-182.
http://dx.doi.org/10.1007/s10750-006-0490-8

Hartel T., Nemes S., Ollerer K., Cogalniceanu D., Moga C., Arntzen J.W. (2010). Using connectivity metrics and niche modelling to explore the occurrence of the northern crested newt *Triturus cristatus* (Amphibia, Caudata) in a traditionally managed landscape. Environmental Conservation 37: 195-200.
http://dx.doi.org/10.1017/s037689291000055x

Hastie T.J., Tibshirani R.J. (1986). Generalized additive models. Statistical Science 1: 297-318.

Hecnar S.J., McLoskey R.T. (1996). Regional dynamics and the status of amphibians. Ecology 77: 2091-2097.
http://dx.doi.org/10.2307/2265703

Heikinheimo O. (1915). Kaskiviljelyksen vaikutus Suomen metsiin. Acta Forestalia Fennica 4: 1-264.

Hotanen J-P., Nousiainen H., Mäkipää R., Reinikainen A., Tonteri T. (2008). Metsätyypit - opas kasvupaikkojen luokitteluun. Metsäkustannus, Hämeenlinna. ISBN 9789525694222. 192 p.

Houlahan J.E., Findlay C.S. (2003). The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences 60: 1078-1094.
http://dx.doi.org/10.1139/f03-095

Houlahan J.E., Findlay C.S., Schmidt B.R., Meyer A.H., Kuzmin S.L. (2000). Quantitative evidence for global amphibian population declines. Nature 404: 752-755.
http://dx.doi.org/10.1038/35008052

Jehle R. (2000). The terrestrial summer habitat of radio-tracked great crested newts (*Triturus cristatus*) and marbled newts (*T. marmoratus*). Herpetological Journal 10: 137-142.

Jehle R., Arntzen J.W. (2000). Post-breeding migrations of newts (*Triturus cristatus* and *T. marmoratus*) with contrasting ecological requirements. Journal of Zoology 251: 297-306.
http://dx.doi.org/10.1111/j.1469-7998.2000.tb01080.x

Jehle R., Bouma P., Sztatecsny M., Arntzen J.W. (2000). High aquatic niche overlap in the newts *Triturus cristatus* and *T. marmoratus* (Amphibia, Urodela). Hydrobiologia 437: 149-155.
http://dx.doi.org/10.1023/a:1026554907400

Joly P., Miaud C., Lehmann A., Grolet O. (2001). Habitat matrix effects on pond occupancy in newts. Conservation Biology 15: 239-248.
http://dx.doi.org/10.1046/j.1523-1739.2001.99200.x

Jylha K., Fronzek S., Tuomenvirta H., Carter T.R., Ruosteenoja K. (2008). Changes in frost, snow and Baltic sea ice by the end of the twenty-first century based on climate model projections for Europe. Climatic Change 86: 441-462.
http://dx.doi.org/10.1007/s10584-007-9310-z

Jylhä K., Ruosteenoja K., Räisänen J., Venäläinen A., Tuomenvirta H., Ruokolainen L., Saku S., Seitola T. (2009). Arvioita Suomen muuttuvasta ilmastosta sopeutumistutkimuksia varten. ACCLIM-hankkeen raportti 2009. Ilmatieteen laitos, Helsinki. ISBN 978-951-697-700-6. Raportteja 2009:4. 102 p.

Karlsson T., Betzholtz P-E., Malmgren J.C. (2007). Estimating viability and sensitivity of the great crested newt *Triturus cristatus* at a regional scale. Web Ecology 7: 63-76.

Kinne O. (2006). Successful re-introduction of the newts *Triturus cristatus* and *T. vulgaris*. Endangered species research 1: 25-40.

Knutson M.G., Richardson W.B., Reineke D.M., Gray B.R., Parmelee J.R., Weick S.E. (2004). Agricultural ponds support amphibian populations. Ecological Applications 14: 669-684.
http://dx.doi.org/10.1890/02-5305

Kovar R., Brabec M., Vita R., Bocek R. (2009). Spring migration distances of some Central European amphibian species. Amphibia-Reptilia 30: 367-378.

Kupfer A., Kneitz S. (2000). Population ecology of the great crested newt (*Triturus cristatus*) in an agricultural landscape: Dynamics, pond fidelity and dispersal. Herpetological Journal 10: 165-171.

Lakka J., Kouki J. (2009). Patterns of field layer invertebrates in successional stages of managed boreal forest: Implications for the declining capercaillie *Tetrao urogallus* L. population. Forest Ecology and Management 257: 600-607.
http://dx.doi.org/10.1016/j.foreco.2008.09.042

Lamoureux V.S., Maerz J.C., Madison D.M. (2002). Premigratory autumn foraging forays in the green frog, *Rana clamitans*. Journal of Herpetology 36: 245-254. http://dx.doi.org/10.1670/0022-1511(2002)036[0245:paffit]2.0.co;2

Lande R. (1988). Genetics and demography in biological conservation. Science 241: 1455-1460.
http://dx.doi.org/10.1126/science.3420403

Lehmann A., Overton J.M., Leathwick J.R. (2003). GRASP: generalized regression analysis and spatial prediction. Ecological Modelling 160: 165-183. http://dx.doi.org/10.1016/s0304-3800(02)00354-x

Leibowitz S.G., Brooks R.T. (2008). Hydrology and landscape connectivity of vernal pools. In: Calhoun A.J.K., DeMaynadier P.G. (eds.) Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton. p. 31-53.

Liikennevirasto (2012). Digiroad. http://www.digiroad.fi/en_GB/. [Cited 4 July 2013].

Lips K.R., Brem F., Brenes R., Reeve J.D., Alford R.A., Voyles J., Carey C., Livo L., Pessier A.P., Collins J.P. (2006). Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proceedings of the National Academy of Sciences of the United States of America 103: 3165-3170. http://dx.doi.org/10.1073/pnas.0506889103

Maaseutuvirasto (2009). Peltolohkorekisteri. http://www.paikkatietoikkuna.fi. [Cited 4 July 2013].

Malmgren J.C., Andersson P.A., Ekdahl S. (2007). Modelling terrestrial interactions and shelter use in great crested newts (*Triturus cristatus*). Amphibia-Reptilia 28: 205-215. http://dx.doi.org/10.1163/156853807780202431

Marsh D.M., Trenham P.C. (2001). Metapopulation dynamics and amphibian conservation. Conservation Biology 15: 40-49.
http://dx.doi.org/10.1046/j.1523-1739.2001.00129.x

Mazerolle M.J., Desrochers A. (2005). Landscape resistance to frog movements. Canadian Journal of Zoology-Revue Canadienne De Zoologie 83: 455-464. http://dx.doi.org/10.1139/z05-032

Metla (2012). Valtakunnan metsien inventointi - metsävaratilastot. http://www.metla.fi/metinfo/vmi/index.htm. [Cited 13 August 2013].

Murton K.M. (2009). Phenological change in palmate (*Lissotriton helveticus*), smooth (*L. vulgaris*) and great crested (*Triturus cristatus*) newts at Llysdinam pond in mid-Wales. Doctoral Dissertation. UMI Dissertation Publishing, Cardiff University. 272 p.

Müllner A. (2001). Spatial patterns of migrating great crested newts and smooth newts: The importance of the terrestrial habitat surrounding the breeding pond. In: Krone A. (ed.)

Der Kammmolch (*Triturus cristatus*) Verbreitung, Biologie, Ökologie and Schutz. p. 279-293.

Nystrom P., Hansson J., Mansson J., Sundstedt M., Reslow C., Brostrom A. (2007). A documented amphibian decline over 40 years: Possible causes and implications for species recovery. Biological Conservation 138: 399-411. http://dx.doi.org/10.1016/j.biocon.2007.05.007

Oldham R.S., Keeble J., Swan M.J.S., Jeffcote M. (2000). Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). Herpetological Journal 10: 143-155.

Paton P.W.C., Crouch W.B. (2002). Using the phenology of pond-breeding amphibians to develop conservation strategies. Conservation Biology 16: 194-204. http://dx.doi.org/10.1046/j.1523-1739.2002.00260.x

Patrick D.A., Harper E.B., Hunter M.L., Calhoun A.J.K. (2008). Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. Ecology 89: 2563-2574. http://dx.doi.org/10.1890/07-0906.1

Patrick D.A., Hunter M.L., Calhoun A.J.K. (2006). Effects of experimental forestry treatments on a Maine amphibian community. Forest Ecology and Management 234: 323-332. http://dx.doi.org/10.1016/j.foreco.2006.07.015

Pechmann J.H.K., Scott D.E., Gibbons J.W., Semlitsch R.D. (1989). Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1: 3-11.

Pellet J., Fleishman E., Dobkin D.S., Gander A., Murphy D.D. (2007). An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. Biological Conservation 136: 483-495. http://dx.doi.org/10.1016/j.biocon.2006.12.020

Ponge J.F. (2003). Humus forms in terrestrial ecosystems: a framework to biodiversity. Soil Biology & Biochemistry 35: 935-945. http://dx.doi.org/10.1016/s0038-0717(03)00149-4

Pounds J.A., Bustamante M.R., Coloma L.A., Consuegra J.A., Fogden M.P.L., Foster P.N., La Marca E., Masters K.L., Merino-Viteri A., Puschendorf R., Ron S.R., Sanchez-Azofeifa G.A., Still C.J., Young B.E. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161-167. http://dx.doi.org/10.1038/nature04246

Pyke C.R. (2004). Simulating vernal pool hydrologic regimes for two locations in California, USA. Ecological Modelling 173: 109-127. http://dx.doi.org/10.1016/j.ecolmodel.2003.08.014

Rainio, H. (1983). The Tuupovaara end moraine in North Karelia, Eastern Finland - an ice marginal formation of the same age as the Salpausselkä ridges. Bulletin of the Geological Society of Finland 55: 67-76.

Raisanen J., Eklund J. (2012). 21st Century changes in snow climate in Northern Europe: a high-resolution view from ENSEMBLES regional climate models. Climate Dynamics 38: 2575-2591.
http://dx.doi.org/10.1007/s00382-011-1076-3

Rannap R., Lohmus A., Briggs L. (2009). Restoring ponds for amphibians: a success story. Hydrobiologia 634: 87-95.
http://dx.doi.org/10.1007/s10750-009-9884-8

Rannap R., Lohmus A., Linnamagi M. (2012). Geographic variation in habitat requirements of two coexisting newt species in Europe. Acta Zoologica Academiae Scientiarum Hungaricae 58: 69-86.

Red Data Book of Estonia (2008). Commission for Nature Conservation of the Estonian Academy of Sciences. http://elurikkus.ut.ee/prmt.php?lang=eng [Cited 26 May 2015].

Rittenhouse T.A.G., Semlitsch R.D. (2006). Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge. Biological Conservation 131: 14-22.
http://dx.doi.org/10.1016/j.biocon.2006.01.024

Rittenhouse T.A.G., Semlitsch R.D. (2007). Postbreeding habitat use of wood frogs in a Missouri oak-hickory forest. Journal of Herpetology 41: 645-653.
http://dx.doi.org/10.1670/07-015.1

Schabetsberger R., Jehle R., Maletzky A., Pesta J., Sztatecsny M. (2004). Delineation of terrestrial reserves for amphibians: post-breeding migrations of Italian crested newts (*Triturus c. carnifex*) at high altitude. Biological Conservation 117: 95-104.
http://dx.doi.org/10.1016/s0006-3207(03)00268-4

Schmidt B.R., Zumbach S. (2005). Rote Liste der gefährdeten Amphibien der Schweiz. Hrsg. Bundesamt für Umwelt, Wald und Landschaft, Bern, und Koordinationsstelle für Amphibien- und Reptilienschutz in der Schweiz. BUWAL-Reihe: Vollzug Umwelt. 48 p.

Semlitsch R.D. (2000). Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64: 615-631.
http://dx.doi.org/10.2307/3802732

Semlitsch R.D. (2008). Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72: 260-267.
http://dx.doi.org/10.2193/2007-082

Semlitsch R.D., Bodie J.R. (2003). Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17: 1219-1228. http://dx.doi.org/10.1046/j.1523-1739.2003.02177.x

Semlitsch R.D., Scott D.E., Pechmann J.H.K., Gibbons J.W. (1993). Phenotypic variation in the arrival time of breeding salamanders - individual repeatability and environmental influeneces. Journal of Animal Ecology 62: 334-340. http://dx.doi.org/10.2307/5364

Semlitsch R.D., Wilbur H.M. (1988). Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. Copeia 4: 978-983.

Sinsch U. (1990). Migration and orientation in anuran amphibians. Ethology Ecology & Evolution 2: 65-79.

Skei J.K., Dolmen D., Ronning L., Ringsby T.H. (2006). Habitat use during the aquatic phase of the newts *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) in central Norway: proposition for a conservation and monitoring area. Amphibia-Reptilia 27: 309-324.

Skelly D.K., Richardson J.L. (2010). Larval sampling. In: Dodd Jr. C.K. (ed.) Amphibian Ecology and Conservation, A Handbook of Techniques, Oxford. p. 55-70.

Skelly D.K., Werner E.E., Cortwright S.A. (1999). Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80: 2326-2337. http://dx.doi.org/10.1890/0012-9658(1999)080[2326:ltddoa]2.0.co;2

Smith K.J., Keeton W.S., Twery M.J., Tobi D.R. (2008). Understory plant responses to uneven-aged forestry alternatives in northern hardwood-conifer forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 38: 1303-1318. http://dx.doi.org/10.1139/x07-236

Smith M.A., Green D.M. (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28: 110-128.

Snodgrass J.W., Bryan A.L., Burger J. (2000). Development of expectations of larval amphibian assemblage structure in southeastern depression wetlands. Ecological Applications 10: 1219-1229. http://dx.doi.org/10.2307/2641028

Stevens V.M., Leboulenge E., Wesselingh R.A., Baguette M. (2006). Quantifying functional connectivity: experimental assessment of boundary permeability for the natterjack toad (*Bufo calamita*). Oecologia 150: 161-171. http://dx.doi.org/10.1007/s00442-006-0500-6

Stuart S.N., Chanson J.S., Cox N.A., Young B.E., Rodrigues A.S.L., Fischman D.L., Waller R.W. (2004). Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783-1786. http://dx.doi.org/10.1126/science.1103538

SYKE (2013). Uomaverkosto. http://www.ymparisto.fi/oiva. Suomen ympäristökeskus. [Cited 3 December 2013].

Sztatecsny M., Schabetsberger R. (2005). Into thin air: vertical migration, body condition, and quality of terrestrial habitats of alpine common toads, *Bufo bufo*. Canadian Journal of Zoology-Revue Canadienne De Zoologie 83: 788-796. http://dx.doi.org/10.1139/z05-071

Temple H.J., Cox N.A. (2009). European Red List of Amphibians. Office for Official Publications of the European Communities Union, Luxemburg. ISBN 978-92-79-11356-7. 33 p.

Terhivuo J., Mannerkoski I. (2010). Matelijat ja sammakkoeläimet. In: Rassi P., Hyvärinen E., Juslén A., Mannerkoski I. (eds.) The 2010 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki. p. 332-335.

Tikkanen M., Oksanen J. (2002). Late Weichselian and Holocene shore displacement history of the Baltic Sea in Finland. Fennia 180: 9-20.

Tilman D., May R.M., Lehman C.L., Nowak M.A. (1994). Habitat destruction and the extinction debt. Nature 371: 65-66. http://dx.doi.org/10.1038/371065a0

Trenham P.C., Koenig W.D., Mossman M.J., Stark S.L., Jagger L.A. (2003). Regional dynamics of wetland-breeding frogs and toads: Turnover and synchrony. Ecological Applications 13: 1522-1532. http://dx.doi.org/10.1890/02-5206

Van Buskirk J. (2005). Local and landscape influence on amphibian occurrence and abundance. Ecology 86: 1936-1947. http://dx.doi.org/10.1890/04-1237

Van Buskirk J. (2012). Permeability of the landscape matrix between amphibian breeding sites. Ecology and Evolution 2: 3160-3167. http://dx.doi.org/10.1002/ece3.424

Wareborn I. (1992). Changes in the land mollusk fauna and soil chemistry in an inland district in southern Sweden. Ecography 15: 62-69. http://dx.doi.org/10.1111/j.1600-0587.1992.tb00009.x

Verrell P., Halliday T. (1985). The population dynamics of the crested newt *Triturus cristatus* at a pond in southern England. Holarctic Ecology 8: 151-156.

Weyrauch S.L., Grubb T.C. (2004). Patch and landscape characteristics associated with the distribution of woodland amphibians in an agricultural fragmented landscape: an information-theoretic approach. Biological Conservation 115: 443-450. http://dx.doi.org/10.1016/s0006-3207(03)00161-7

Wiens J.A. (2006). Introduction: Connectivity research - what are the issues? In: Crooks K.R., Sanjayan M. (eds.) Connectivity Conservation. Cambridge University press, Cambridge. p. 23-28.

Vlašín M. (2003). Reptiles and Amphibians. In: Witkowski Z.J., Król W., Solarz W. (eds.) Carpathian List of Endangered Species. WWF and Institute of Nature Conservation, Polish Academy of Sciences, Vienna-Krakow. p. 32-34.

Vos C.C., Chardon J.P. (1998). Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology 35: 44-56.

Vuorio V. (2009). Suomen uhanalaisia lajeja: Rupilisko (*Triturus cristatus*). Suomen ympäristö 34/2009. Pohjois-Karjalan ympäristökeskus, Joensuu. ISBN 978-952-11-3561-3. p. 98.

Vuorio V., Heikkinen R.K., Tikkanen O-P. (2013). Breeding success of the threatened great crested newt in boreal forest ponds. Annales Zoologici Fennici 50: 158-169.

Vuorio V., Tikkanen O-P., Mehtatalo L., Kouki J. (2015). The effects of forest management on terrestrial habitats of a rare and a common newt species. European Journal of Forest Research 134: 377-388. http://dx.doi.org/10.1007/s10342-014-0858-7

Yrjölä T. (2002). Forest management guidelines and practices in Finland, Sweden and Norway. European Forest Institute. Internal Report 11. 46 p.

Zenner E.K., Lahde E., Laiho O. (2011). Contrasting the temporal dynamics of stand structure in even- and uneven-sized *Picea abies* dominated stands. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 41: 289-299. http://dx.doi.org/10.1139/x10-205