Choosing the Best of Both Worlds

The Double Life of the Great Crested Newt

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Abstract

The great crested newt (*Triturus cristatus*) is dependent on two environments for its survival: the aquatic habitat necessary for breeding and development, and the terrestrial habitat required for post-breeding and juvenile activities. For a population to be able to survive in a landscape, both habitat types must be present within migration distance from each other. The overall aim of this thesis is to find and describe prerequisites of environments and landscapes that make them sufficient as habitats for the great crested newt. The purpose is also to present the results in a conservation perspective and to discuss them in relation to practical examples. In five separate studies, performed in Örebro County, south-central Sweden, the aquatic and terrestrial habitats of the species were examined. The first study examined aquatic plants in a variety of ponds and landscapes, to determine if the diversity of plant species was higher in ponds where great crested newts were present. I found that ponds with newts had a significantly higher mean number of plant species than ponds without the species. The second study focused on the question if there are chemical and physical characteristics that determine occurrence of great crested newts. The results showed that temperature and nutrient levels (nitrogen and phosphorus) were important in distinguishing between ponds with and without newts, whereas other physical variables were less important. My results also suggest that the great crested newt selects ponds with low nutrient levels for breeding, while the species may also be present in ponds with higher nutrient levels. The third study used radio-telemetry in an attempt to determine how the great crested newt moved in its terrestrial habitat and which micro-habitats it used while the focal point of study four was the landscape and if landscape composition may predict use of ponds as aquatic habitats. Combined, studies three and four suggest that management of the species should to a greater extent include terrestrial habitat, with special attention given to older, deciduous-rich forest within approximately 200 m of breeding ponds. The aim of the last study was to describe and evaluate a project concerning translocation of a great crested newt population. I point out the necessity of long-term monitoring to distinguish any possible success with respect to site sustainability and population size.

Keywords: Amphibia, Caudata, *Triturus cristatus*, aquatic and terrestrial habitat use, landscape, pondscape, indicator species, radio-telemetry, translocation

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Dedication

Till min far Claes-Håkan Gustafson

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Gustafson, D.H., Journath Pettersson, C. & Malmgren, J.C. (2006). Great crested newts (Triturus cristatus) as indicators of aquatic plant diversity. *Herpetological Journal* 16(4), 347-352.

II Gustafson, D.H., Andersen, A.S.L., Mikusiński, G. & Malmgren, J.C. (2009). Pond quality determinants of occurrence patterns of great crested newts (Triturus cristatus). *Journal of Herpetology* 43(2), 300-310.

III Gustafson, D.H., Malmgren, J.C & Mikusiński, G. Terrestrial movement and habitat use of great crested newts (Triturus cristatus) (manuscript).

IV Gustafson, D.H., Malmgren, J.C. & Mikusiński, 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, in press.

V Gustafson, D.H. & Mikusiński, G. When development and amphibians meet – a case study on great crested newts (Triturus cristatus) from south-central Sweden (manuscript).

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The contribution of Daniel Gustafson to the papers included in this thesis was as follows:

I 50 %

II 50 %

III 60 %

IV 75 %

V 85 %

1 Introduction

The great crested newt (*Triturus cristatus*) is an amphibian species that is declining throughout its distribution range (Kuzmin, 1994; Beebee, 1997; Beebee and Griffiths, 2000; Edgar and Bird, 2006). This is a trend that can be found among many amphibian species all over the world (Houlahan et al., 2000; Stuart et al., 2004; D´Amen and Bombi, 2009). The reasons for diminishing amphibian populations has been investigated and disputed widely and appear to vary among species in different parts of the world (Griffiths et al., 1996; Houlahan et al., 2000; Stuart et al., 2004; Beebee and Griffiths, 2005; D´Amen et al., 2010). Possible causes for these declines include habitat alteration, over-exploitation, introduction of alien species, changing climate, diseases and emissions of environmental hazards (Kiesecker et al., 2001; Teixeira and Arntzen, 2002; Collins and Storfer, 2003; Lips et al., 2005; Cushman, 2006; Hamer and McDonnell, 2008).

In Europe, the most evident causes for decreasing numbers and loss of populations are habitat destruction and landscape fragmentation, followed by pollution with climate change, invasive alien species and pathogens (Griffiths et al., 1996; Oldham and Swan, 1997; Wood et al., 2003; Cushman, 2006; Edgar and Bird, 2006; Temple and Cox, 2009). The great crested newt, as well as most pond-breeding amphibians, is dependent on two different habitats: the aquatic habitat necessary for breeding and development, and the terrestrial habitat required for post-breeding activities and during the juvenile phase. These two different habitats must be functionally connected with each other to make dispersal and seasonal migration possible. The interconnectivity and quality of aquatic and terrestrial habitats, as well as the surrounding matrix, are factors that are likely to be of great importance for the great crested newt, but have received little attention (Kupfer and Kneitz, 2000; Joly et al., 2001; Hartel et al., 2010a; Hartel et al., 2010b).

Typical aquatic and terrestrial newt habitats (i.e. small ponds and heterogenic, low intensity use cultural landscapes) are both among those habitat types that have generally decreased in modern landscapes (Bernes, 1994; Ihse, 1995; Hull, 1997; Benton et al., 2003; Löfvenhaft et al., 2004; Loman and Anderson, 2007; Curado et al., 2011). A number of surveys have indicated that several previously known newt localities have been destroyed in this process of landscape change (Beebee and Griffiths, 2000; Edgar and Bird, 2006; Malmgren, 2007). Destruction of habitats causes further isolation and fragmentation of landscapes and affect newts and other amphibians negatively both at the individual and population levels. The metapopulation structure and relatively short migration distance of great crested newts makes them particularly vulnerable to habitat alterations (Laan and Verboom, 1990; Joly et al., 2001; Ficetola and De Bernardi, 2004; Schabetsberger et al., 2004; Karlsson et al., 2007). To be able to prevent further destruction and deterioration of habitats, and in order to successfully restore and construct suitable habitats, it is crucial to learn which factors influence habitat selection, survival and reproduction of the great crested newt. In the characterization of the aquatic habitat, physical and chemical, as well as biological characteristics should be regarded (Gustafson et al., 2006; Gustafson et al., 2009). When studying the terrestrial habitat of the species, it is also important to consider different spatial scales and distances from an aquatic habitat (Gustafson et al., 2011).

The great crested newt is included in Annex II of the European Habitats Directive, which requires designation of protected areas for the species. A clear understanding of the habitat requirements of the species is therefore a necessary prerequisite in assessing its conservation status and in management and development planning. Moreover, the species might also be a suitable indicator or umbrella species for other pond-breeding amphibians and for pond-dwelling biodiversity, which presumably makes it useful as an important tool for monitoring of amphibian habitats and landscapes (Caro and O´Doherty, 1999; Roberge and Angelstam, 2004; Gustafson et al., 2006; Malmgren, 2007). Such ‘indicator species’ are assumed to mirror changes in population processes, species distributions and viability in other taxa, at both local and regional scales, thus providing a tool for measuring and monitoring effects on biodiversity (Pearson, 1995). The biphasic life-cycle of amphibians may make them particularly useful as indicators of biodiversity changes in pond landscapes, since they are vulnerable to habitat alterations and environmental stress (Houlahan et al., 2000). However, amphibian population dynamics are often influenced by processes acting at different scales and therefore studies should include the effects of multiple factors that potentially affect the general habitat quality.

The overall aim of this thesis is to find and describe prerequisites of environments and landscapes that make them sufficient as habitats for the great crested newt. The purpose is also to present the results in the perspective of conservation measures and to integrate them with practical examples. In five separate studies, performed in Örebro County, south-central Sweden, the aquatic and terrestrial habitats of the great crested newt were examined. The first two studies included in this thesis add to the knowledge concerning the aquatic habitat of the great crested newt. **Paper I** examines the value of the great crested newt as an indicator species for species-rich habitats, specifically in relation to aquatic plants. **Paper II** evaluates how different chemical and physical parameters interact to define habitat suitability to great crested newts. The next two papers describe the terrestrial habitat of the great crested newt from several different perspectives. First, **Paper III** investigates the terrestrial habitat from a local perspective, using radio-telemetry to track great crested newts when moving from their aquatic habitat towards their terrestrial habitat. Second, **Paper IV** examines structure and composition of landscapes surrounding ponds with and without great crested newts. Finally, **Paper V** takes a more practical conservation approach and describes and discusses a translocation case of a great crested newt population.

2 Life and habits of the great crested newt

2.1 Systematics and morphology

Newts and salamanders are tailed amphibians (Amphibia: Caudata) and belong to the family Salamandridae. Newts are often separated from other salamanders by having a well-defined aquatic phase as breeding adults (Griffiths, 1996; Malmgren, 2001). There are 14 species of newts in Europe, divided into four genera (Malmgren, 2001; Miller, 2004; Thiesmeier and Grossenbacher, 2004). Out of these, only two are found in Scandinavia: the smooth newt (*Lissotriton vulgaris*) and the great crested newt (*Triturus cristatus*) (Fig. 1).

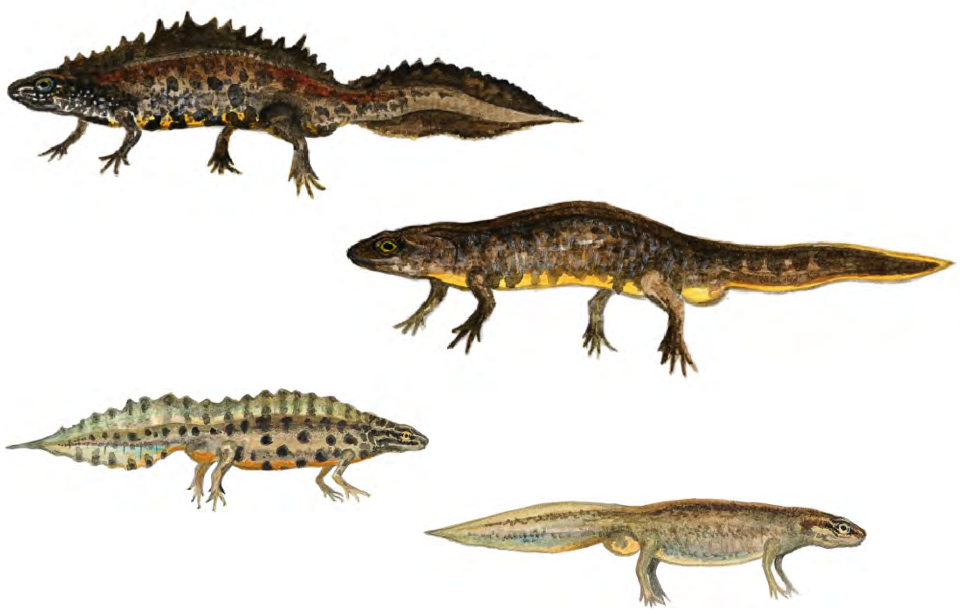

Figure 1. Images of great crested newts *Triturus cristatus* (above) and smooth newts *Lissotriton vulgaris* (below); males to the left and females to the right (courtesy of Per Wedholm).

Adult great crested newts can be as large as 16 to 18 cm from snout to tail-tip, compared with the smooth newt, which is usually smaller than 10 cm (Griffiths, 1996; Thiesmeier and Kupfer, 2000). Usually, the size of adult great crested newts is between 11 and 15 cm and females are generally larger than males (Griffiths, 1996; Malmgren and Thollesson, 1999). Apart from differences in size, colour and other skin characters make it easy to separate between the two species.

In the aquatic phase male great crested newts develop a serrated crest on the back and on the tail. Furthermore, a shimmering silver stripe is pronounced along the sides of the tail. These characters are used to attract females during courtship displays (Malmgren and Enghag, 2008). Females lack these features, but the height of their tail increases slightly. The eggs are laid separately and are wrapped in leaves of sub-aquatic plants. These features make newt eggs easy to distinguish from eggs of frogs and toads. The egg cell of the great crested newt is light in coloration and approximately 2 mm in diameter, covered by a thin gelatinous layer making the eggs totally 4-5 mm wide (Fog et al., 2001). Larvae of great crested newts have a long tail that ends with a black elongated tip. On the crest and tail there are black spots. Larvae of newts have external gills that are placed laterally in the neck region of the head. These are successively lost prior to metamorphosis. When the newts are ready to enter the terrestrial stage their body length is between 40 to 90 mm and have a miniaturized adult appearance.

2.2 Geographic distribution

Newts and salamanders have a global distribution, and are found on all continents except Australia and Antarctica (Griffiths, 1996). The great crested newt has a distribution range throughout northern and central Europe extending east to the Ural Mountains (Griffiths, 1996; Gasc et al., 1997; Arntzen, 2003). The distribution shows pronounced division and isolation of separate populations (Gasc et al., 1997; Thiesmeier and Kupfer, 2000). In Scandinavia, the species can be found throughout almost entire southern Sweden, and its occurrence is extending north to the counties of Jämtland and Ångermanland (Fig. 2). At least until the middle of the 20th century the northernmost occurrence for the great crested newt was confirmed as far north as at 65^{o} latitude in Stensele in central Lappland (Dolmen, 1978). In Norway, the great crested newt is established in three separate areas: around the Oslo fiord in the south-east, in the Bergen area in the south-west, and in the Trondheim area in the central part (Dolmen, 1982). The species can also be found in the Baltic archipelago of Åland and in Karelia in the eastern part of Finland (connected with the distribution range in Russia) (Terhivuo, 1993).

In Sweden, the great crested newt has quite an irregular distribution (Fig. 2). It is more or less evenly distributed in the southern part of the country, extending north to the *Limes Norrlandicus* (approximately 60^o N latitude). North of this rather abrupt border the species is found mainly along the coast, and as relic populations further inland. As Sweden lies on the northern distribution limit of the great crested newt, the species is more common in the south and particularly along the coasts, and further north generally occurs in areas with warmer local climate (Dolmen, 1982; Malmgren, 2007). Moreover, the majority of the populations in Scandinavia are situated on lower elevation, up to a height of approximately 200 m above sea level, although a few Norwegian populations have been found at altitudes between 400-600 m above sea level (Dolmen, 1982).

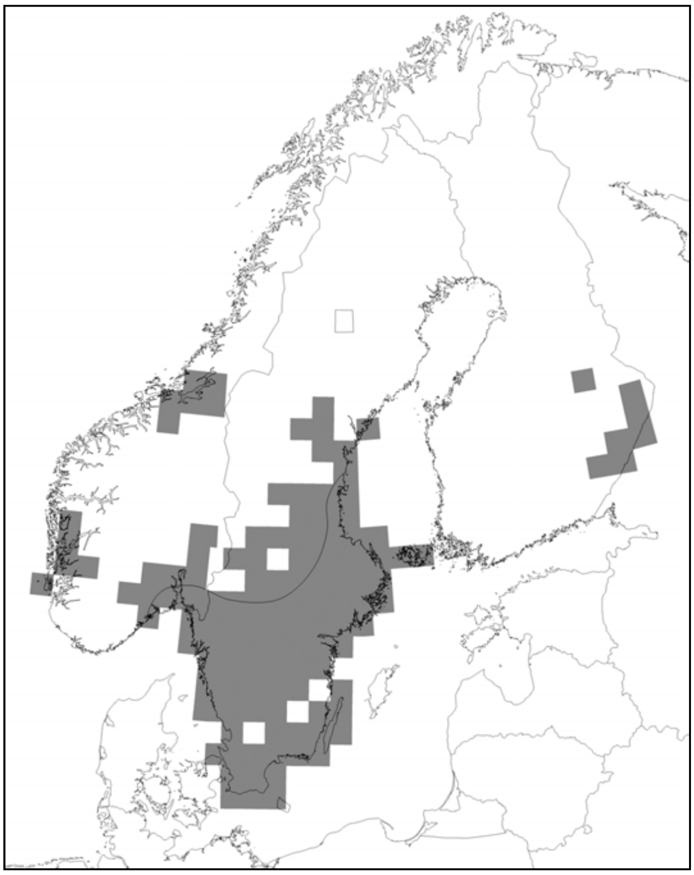

Figure 2. Map showing the presently known distribution (including observations made in 2008) of the great crested newt in Fennoscandia (courtesy of Jan Malmgren, unpubl.).

In recent surveys in the northern Swedish counties of Jämtland, Dalarna and Gästrikland, and in the highlands of southern Sweden, several previously unknown localities with relic populations have been found (e.g. Johansson et al., 2005; Andersson et al., 2008). The irregular distribution and abrupt northern distribution limit of the great crested newt in Scandinavia might ultimately be linked to survey frequency, or rather infrequency. As the species has not been thoroughly surveyed throughout the country, it is still difficult to assess the true distribution pattern.

2.3 Ecology

Similar to many other amphibians, the great crested newt has both terrestrial and aquatic phases, tied to specific aquatic and terrestrial habitats. The aquatic habitat is used for courtship, breeding and larval development, and is only occasionally visited by juveniles. The rest of the life-cycle, including over-wintering, is spent in the terrestrial habitat. Breeding takes place during spring and early summer; in Scandinavia from late April to the beginning of June (Malmgren, 2007). Newts awake from hibernation with the end of ground frost and when the temperature rises above approximately $0^{o}C$ (Malmgren, 2002). Migration towards the aquatic habitat often starts during the first warm nights of spring, usually during rain. Before and while arriving to the aquatic habitat individuals adjust morphologically and physiologically to life in the water and when water temperature rises above approximately $10^{o}C$ courtship begin (Thiesmeier and Kupfer, 2000; Malmgren, 2007).

The courtship of the great crested newt is rather intriguing. Courtship takes place mainly at night and seems to be most intense from dusk to midnight. Male newts gather in groups in preferred places (often open areas surrounded by vegetation) close to the shoreline, at a depth of 20 to 60 cm (Thiesmeier and Kupfer, 2000). Trying to establish a favourable place at a courtship arena, males swim or walk around to show off their courtship dress and make attacks on each other. When a female arrives one or a few males usually start to court her. The courtship involves mutual interactions in several different stages, but it ends with one male delivering a spermatophore to the female (Hedlund, 1990; Malmgren, 2001). The female picks up the spermatophore in her cloaca, from where the sperms wander to the oviduct where the eggs are fertilized. Females mate many times with different males during the courtship period, to avoid lack of sperm for the fertilization of her eggs (Hedlund, 1990; Malmgren, 2007). At the beginning of the courtship period females are very selective, and choose males that are large and have conspicuous crests

(Malmgren and Enghag, 2008), but at the end of the season they are less choosy (Malmgren, 2007).

Females lay their eggs separately on carefully selected places in the submerged vegetation in shallow water (Miaud, 1995). Eggs are placed on leaves and the female then wrap them in packages, which helps in protecting them from predators and solar radiation (Miaud, 1993; Miaud, 1994; Langhelle et al., 1999; Marco et al., 2001). For egg-laying, newts seem to prefer plants with soft and thin leaves as for example sweet or flote grasses (*Glyceria* spp.), water mint (*Mentha aquatica*), water forget-me-not (*Myosotis scorpioides*) and broad-leaved pond weed (*Potamogeton natans*) (Langton et al., 2001; **Paper I**). A female can lay approximately 200 to 300 eggs during a season and between 5 and 15 eggs every day (Thiesmeier and Kupfer, 2000; Langton et al., 2001). When all eggs are laid, and the courtship period has come to an end, all adults leave the pond. In Scandinavia, the majority of the adult newts leave the pond in June or July (Malmgren, 2002).

The development from egg to free-living larvae takes approximately 2 to 3 weeks, depending mostly on water temperature. Due to inherent defects, half of the embryos fail to develop to the larval stage (Macgregor and Horner, 1980; Malmgren, 2001). Newt larvae are predators, and during early development they seem to prefer planktonic crustaceans (Dolmen and Koksvik, 1983). Later they also feed on larger aquatic invertebrates, like nymphs of aquatic beetles and mayflies, mosquito larvae or leeches and molluscs. They may also predate on larvae of other amphibian species or even of their own species (Griffiths and Mylotte, 1987; Griffiths et al., 1994; Griffiths, 1996). Newt larvae are in turn exposed to predation from fish, dragonfly nymphs and water beetles (Miaud, 1993; Cooke, 2001). For protection, they often hide in the vegetation or at the bottom of the pond. Presence of predatory fish is quite disastrous for eggs and larvae, and may even exclude occurrence of great crested newts in a pond (Cooke and Frazer, 1976; Thiesmeier and Kupfer, 2000; Malmgren, 2001). When adult newts select breeding habitat, they appear to avoid water with fish presence (Malmgren, 2001). Newts probably use chemical cues to detect fish, and actively select alternative breeding ponds when such are available (Malmgren, 2001), which is not always the case in modern landscapes.

After approximately four months of development, the outer gills of the larvae are resorbed, and they start to use lungs for breathing. Concurrently, other morphological features prepare the young newts to a terrestrial life (for example the skin thickens and adapts to terrestrial conditions). From August to October or even November, metamorphs migrate from the aquatic habitat to start a terrestrial life (Malmgren, 2007). Since egg-laying is prolonged, migration is not synchronized, but it is most intensive during warm nights with rain (Thiesmeier and Kupfer, 2000; Malmgren, 2001; Malmgren, 2002). Great crested newts become sexually mature at the age of 2-3 years (Griffiths, 1996). Immature individuals most often stay in their terrestrial habitat during this period, but may also return to their natal pond even before reaching an adult stage (Griffiths, 1996; Langton et al., 2001).

When the reproductive period is over, adult newts start an active period in their terrestrial habitat. After leaving the pond, individuals seem to move quickly seeking protection in suitable terrestrial environments (**Paper III**). While in their terrestrial phase, great crested newts probably consume mainly worms, centipedes, woodlice and insect larvae (Griffiths, 1996; Thiesmeier and Kupfer, 2000). Adult and juvenile newts are exposed to a number of potential predators, both in their aquatic and terrestrial habitat. These include snakes, birds and mammals (Gleed-Owen, 1996; Jehle and Arntzen, 2000; Thiesmeier and Kupfer, 2000; Webley, 2007). However, the species is to some extent protected by the presence of granular glands in the skin, which may release poisonous secretions. Great crested newts are mainly nocturnal and lead a cryptic life, especially in their terrestrial phase where they mostly move and hide among for example leaf litter, logs and stones or in underground cavities (Jehle, 2000; Jehle and Arntzen, 2000; Schabetsberger et al., 2004; **Paper III**). This behaviour is probably in part predator avoidance but also due to their sensitivity for desiccation (but see also Malmgren et al., 2007). Structures and microhabitats such as dead wood and leaf litter are also abundant resources of prey (Bobiek et al., 2005). When temperatures fall below approximately 2^{o}C newts seek refuge for hibernation (Griffiths, 1996). Adequate refuge sites are probably constituted by deeper and warmer sites than the daily hideouts used during the rest of the year. Newts may also seek hibernation sites in human made structures, such as stone fences and cellars (Thiesmeier and Kupfer, 2000; Jehle and Arntzen, 2001). The length of the hibernation period is most likely determined by temperature and rainfall. In field population studies individuals that are up to 16 or 17 years old can sometimes be found (Hagström, 1979; Dolmen, 1982; Thiesmeier and Kupfer, 2000).

3 Threats and conservation

More than one-third of the known amphibian species of the world are threatened and, as stated above, there are many potential reasons for this cataclysm (Griffiths et al., 1996; Stuart et al., 2004; Cushman, 2006; IUCN, 2011). Moreover, more than half of all European amphibian species are declining in population (Temple and Cox, 2009). Population declines of the great crested newt have been observed throughout Europe, as for example in Great Britain (Beebee, 1997; Beebee and Griffiths, 2000), Norway (Dolmen, 1982), Germany (Thiesmeier and Kupfer, 2000), Austria (Thiesmeier and Kupfer, 2000) and the former Soviet Union (Kuzmin, 1994). Since the knowledge of the actual distribution of the great crested newt in Sweden is incomplete, it is difficult to draw far-reaching conclusions about its conservation status. Nevertheless, a large survey effort in recent years has shown that the species is more widely distributed than previously thought (e.g. Hellberg et al., 2004; Johansson et al., 2005; Andersson et al., 2008). As mentioned earlier, this increase in number of known localities gives a more legible picture of the actual distribution of the species, and a more precise understanding of the historical distribution is now beginning to emerge. However, it is important to stress that the observed increase in the amount of observations is not evidence for a population increase or a more favourable conservation status. Other studies have shown that the contrary is probably more correct. For example, in 2005 a re-survey was made in 296 ponds with previously known presence of great crested newts (observations made from 1980 and forward), in four counties in the south-central parts of Sweden (Malmgren, 2007). The results from this survey showed that the species was absent from approximately 30 % of the surveyed ponds. The results show that the species is in decline also in Sweden, in rates comparable to that observed in other countries (Thiesmeier and Kupfer, 2000; English Nature, 2001; Edgar and Bird, 2006). However, in some parts of Sweden (especially Skåne), where several hundreds of ponds have been created and restored, the species may actually be in a state of recovery (Stenberg and Nyström, 2008).

Large-scale changes in landscape structure and land-use during the last 200 years have resulted in a great loss of structurally and compositionally diverse landscapes throughout the distribution area of the great crested newt (e.g. Bernes, 1994; Ihse, 1995; Hull, 1997; Stoate et al., 2009). For example, Hull (1997) reported a 40-90 % reduction in pond numbers during the 20th century in several countries in north-western Europe. Different kinds of wetlands have been ditched, cultivated and/or forested. In more recent years, many small ponds in agricultural landscapes that were previously used for e.g. providing water to cattle or fire extinguishing, have been filled up and replaced by wells and tapped water. Development, for example in the form of infrastructure, new industries, residential areas etc., are also negative factors causing ponds to disappear, especially in the vicinity of towns and cities (Hamer and McDonnell, 2008; **Paper V**). All this results in a large decrease of aquatic habitat for the great crested newt and destruction of ponds is still one of the most common causes for disappearance of great crested newt populations (Beebee, 1997; Thiesmeier and Kupfer, 2000; Malmgren, 2007).

The quality of remaining potential habitats is also affected by changes in the landscape and by changes in the practical use of ponds and small waters (Houlahan and Findlay, 2004; Denoël and Ficetola, 2008). Amphibians are in general regarded as being highly susceptible to environmental pollutants, due to physiological requirements and their biphasic life cycle, and this also applies to the great crested newt (Blaustein et al., 1994; Griffiths and DeWijer, 1994; Thiesmeier and Kupfer, 2000; Skei et al., 2006). Ponds in agricultural landscapes are to a great extent affected by chemicals and nutrients from nearby fields and pastures (Brönmark and Hansson, 1998; Relyea, 2005; Kadoya et al., 2011). Consequently, eutrophication is a problem in landscapes with extensive farming and use of artificial fertilizers. A large influx of nutrients and a reduced use of agricultural ponds and semi-natural pastures (e.g. by grazing) speed up the natural process of overgrowth of ponds and their surroundings (Oldham, 1994; Brönmark and Hansson, 1998; Brönmark and Hansson, 2002). As indicated by **Paper I** and other studies, this severely decreases the quality of the aquatic habitat for the great crested newt and other amphibians (Oldham et al., 2000; Sztatecsny et al., 2004; Nyström et al., 2007). Too much inflow of nutrients may also cause an explosive growth of algae, quickly reducing the quality of the aquatic habitat even further (Brönmark and Hansson, 1998; Kadoya et al., 2011). In addition, air pollution deteriorates the quality of the water, lowering pH-values and increasing nutrient contents (Griffiths, 1996; Brönmark and Hansson, 1998; Jeffries, 1998). Introduction of fish into ponds is one of the main reasons for the disappearance of great crested newt populations in several regions (Beebee, 1985; Baker and Halliday, 1999; Thiesmeier and Kupfer, 2000; Joly et al., 2001).

Afforestation and forest succession in the immediate surroundings of a pond causes shadowing followed by lower temperatures and decreased sun insolation to the aquatic habitat (van Buskirk, 2011). Otherwise, the terrestrial habitat is probably negatively affected by logging of forest, ditching and other forestry measures (Latham and Oldham, 1996; Schabetsberger et al., 2004). The overall reduction of dead wood in forests and pastures reduces the supply of suitable hiding places and food availability. Increased proportions of fields, roads and other inhospitable environments generally decrease the amount of terrestrial habitats for amphibians and increase landscape fragmentation (Swan and Oldham, 1993; Oldham et al., 2000; Fahrig, 2001; Fahrig and Rytwinski, 2009).

Decreasing populations and local extinctions have brought increased awareness of the situation of the great crested newt. Today, the species is protected by law in most European countries within the distribution area, including Sweden (Artskyddsförordningen 2007:845). The great crested newt is also listed on Annexes II and IV of the EC Habitats Directive and Appendix II of the Bern Convention. It is protected under Schedule 2 of the Conservation Regulations 1994 (Regulation 38) and Schedule 5 of the WCA 1981. This means that not only the species itself, but also its habitats are protected. In Sweden, presence of great crested newts may prevent human exploitation of land, if the exploitation is not ”[…] for consideration of public health and safety or for other dire reasons with an all overshadowing public interest” (Artskyddsförordningen 2007:845, 14§). According to the legislation, exemptions may only be made if there are no other appropriate alternatives to destruction of the species´ habitats and if the exemption does not aggravate the maintenance of favourable conservation status of the species in its natural distribution area. In the United Kingdom, Sweden and for entire Europe, species action plans have been produced in order to facilitate and guide conservation measures for the species (Edgar and Bird, 2006; Malmgren, 2007). The species action plan in Sweden have resulted in for example construction and restoration of ponds, and increased public awareness of the species and its prerequisites.

4 Two distinct habitats

As reviewed above, great crested newts are using two different environments: the aquatic habitat and the terrestrial habitat. The most common scenario for amphibians is that they need several habitats to complete their life cycles, including breeding, foraging and hibernation sites (Gibbs, 2000; Semlitsch and Bodie, 2003; Stevens and Baguette, 2008). Most amphibians breed in freshwater habitats and spend the rest of their active period in terrestrial habitats (Skelly et al., 1999; Marsh and Trenham, 2001). The spatial proximity of high quality aquatic and terrestrial habitats in the landscape is the key for the maintenance of viable populations and therefore this perspective is important in conservation work (Latham and Oldham, 1996; Semlitsch, 2002; Ficetola and De Bernardi, 2004).

In Sweden, the great crested newt can be found in a variety of aquatic and terrestrial environments. The species inhabits and breeds in shallow and nutrient-rich waters in agricultural landscapes as well as in deeper and more nutrient-poor ponds surrounded by for example mires and forest landscapes (Hellberg et al., 2004; Malmgren, 2007). While on land, they can be found in deciduous forests with herbaceous undergrowth as well as in coniferous forests with bilberry and lingonberry sprigs. There are still many gaps in knowledge concerning the habitat selection of the species, especially in its terrestrial habitat and on the landscape level. In many areas where habitats have disappeared in great numbers, the species has been forced to cling on to unfavourable aquatic and terrestrial habitats, in lack of better options. Therefore it is often quite difficult to see from present habitat use which types of ponds are actually preferred.

4.1 The aquatic habitat

The aquatic habitat selection of the great crested newt is generally better known and studied than its terrestrial counterpart (e.g. Griffiths, 1996; Thiesmeier and Kupfer, 2000; Malmgren, 2001; Malmgren, 2007). The species is relatively easy to find in its aquatic phase and both reliable and easily applied survey methods exist (Swan and Oldham, 1993; Griffiths et al., 1996; Langton et al., 2001; Malmgren et al., 2005). Furthermore, the aquatic habitat is often better defined in space than the terrestrial habitat. Several factors are of importance when assessing the quality of the aquatic habitat. These include physical, chemical and biological characteristics but also spatial considerations (e.g. juxtaposition in the landscape).

Stagnant water is preferred as aquatic habitat by the great crested newt. A typical habitat for the species seems to be a moderately shallow pond, small lake or tarn with a surface area of approximately 50-250 m^2 (Thiesmeier and Kupfer, 2000; Langton et al., 2001; Sztatecsny et al., 2004; Denoël and Ficetola, 2008). However, great crested newts have also been found breeding in larger and deeper ponds and can occasionally be found along the shores of small lakes (Oldham et al., 2000; Thiesmeier and Kupfer, 2000), so perhaps surface area and depth are characters of secondary importance. To allow for abundant submerged vegetation and higher water temperatures, the shoreline is preferably shallow, with a gentle slope. It is crucial that the habitat holds water at least until the end of the larval development in October or November, but it does not necessarily have to be permanent (Griffiths, 1997; Denoël and Lehmann, 2006; Malmgren, 2007). Periodic drying might instead be positive, as it reduces the abundance of predators and slows down overgrowth with vegetation (Beja and Alcazar, 2003; Ficetola and De Bernardi, 2004).

As described above, the great crested newts are sensitive to predators, especially during embryonic and larval phases. Fish in particular are severe predators, and therefore presence of fish in a pond is a strong negative factor (Beebee, 1985; Baker and Halliday, 1999; Joly et al., 2001; Malmgren, 2001; Skei et al., 2006). Fish may also compete for the same food resources (e.g. invertebrates) and cause changes to the pond ecosystems, which may then become unsuitable for predatory amphibians as the great crested newt (Schabetsberger et al., 2006).

Most studies investigating the biological diversity in ponds and their surroundings have shown that physical, biological and landscape characteristics appear to be more important than chemical characteristics for plants and animals in these aquatic environments (Laan and Verboom, 1990; Pavignano et al., 1990; Sztatecsny, et al., 2004; Denoël and Ficetola, 2007). However, when considering important aquatic habitat parameters, it is important to keep in mind that a variety of physical and chemical variables interact to determine the composition and distribution of life in a pond (Angelibért et al., 2004; Biggs et al., 2005; Scheffer and van Geest, 2006; **Paper II**). Equally important is the opposite – biological factors influence the chemistry and physical parameters of a pond to a large extent (Gustafsson and Boström, 2011), as for example when levels of temperature and oxygen vary as a response to vegetation cover in different stages of pond succession (Angelibért et al., 2004). In addition, cascade effects between species and different levels in the ecosystem may convey unforeseen changes due to small differences in for example levels of nutrients or following presence or absence of certain key species (Aronsson and Stenson, 1995; Cottenie and De Meester, 2004).

4.2 The terrestrial habitat and the pondscape

While on land, great crested newts need foraging opportunities; they need places and structures for refuge during daytime and where they can hibernate. Furthermore, they must be able to move between these different environments and between aquatic and terrestrial habitats. Studies of terrestrial habitat selection of great crested newts are scarce (but see e.g., Jehle, 2000; Jehle and Arntzen, 2000; Joly et al., 2001; Malmgren et al., 2007; Hartel et al., 2010a). While on land the species leads a secretive life. Generally, fewer survey methods are also available for newts in their terrestrial phase. Searching for newts on land is not very effective and often leads to destruction of their habitat, and is therefore seldom performed (Jehle, 2000; Langton et al., 2001). Thus, observations concerning terrestrial habitat use are rarely based on systematic surveys. However, a few studies using radio-transmitters have been performed (Jehle, 2000; Jehle and Arntzen, 2000; Schabetsberger et al., 2004; **Paper III**). Combined, different studies and anecdotal observations indicate that the great crested newt prefers environments with a high coverage in the field vegetation layer and/or with a high quantity of substrate like leaf litter, boulders and logs on the ground. All in all, these structures offer places for hiding and often contain a magnitude of invertebrate prey. Environments where great crested newts are found include forest, deciduous woodland, wetland, semi-natural pastures and grasslands (Griffiths, 1996; Latham and Oldham, 1996; Jehle and Arntzen, 2000; Thiesmeier and Kupfer, 2000; Langton et al., 2001). However, environments such as coniferous forests, gravel pits and even former industrial areas containing construction waste appear to be sufficient terrestrial habitats (Latham and Oldham, 1996; Thiesmeier and Kupfer, 2000; **Paper V**). Possibly, the key characteristic for an environment to be suitable as a terrestrial habitat for the great crested newt is the presence of sufficient microhabitats. Some less optimal terrestrial environments may be used by the species when there are few or no alternatives, due to recent landscape change. Landscape elements that seem to be avoided by great crested newts are for example open fields, where the risk of predation and desiccation probably increases dramatically as there is little coverage and few hiding places (Jehle and Arntzen, 2000; Oldham et al., 2000; Joly et al., 2001; Malmgren, 2002).

Most important for the great crested newt seems to be the quality of the area directly adjacent to a breeding pond (Jehle, 2000; Malmgren, 2002) or within a few hundred meters from the pond (Dolmen, 1982; Latham and Oldham, 1996; Baker and Halliday, 1999; Jehle and Arntzen, 2000; Oldham and Humphries, 2000; **Paper III**). For example, Jehle (2000) showed that 95 % of radio-marked individuals stayed within approximately 60 m from the breeding pond. Newly constructed ponds in areas with great crested newts are quickly colonized if they are located within approximately 500 m from an old pond (Latham and Oldham, 1996; Baker and Halliday, 1999; Kupfer and Kneitz, 2000; Rannap, 2009). Other studies have shown that individuals may migrate up to 1300 m within one year (Kupfer, 1998), which indicate that at least some individuals move over larger distances, given that the landscape matrix allow for dispersal. Juvenile great crested newts may be more eager to migrate longer distances than adults, while adults more often return to the same breeding pond year after year (Arntzen and Wallis, 1991; Kupfer and Kneitz, 2000).

Several studies have shown the importance of metapopulation dynamics for the great crested newt and other amphibian species (Sjögren, 1991; Vos and Chardon, 1998; Joly at al., 2001; Marsh and Trenham, 2001; Semlitsch, 2002; Denoël and Lehmann, 2006). Migrating behaviour promotes dispersal and is probably more common in populations with high-quality aquatic habitats that produce a surplus of individuals (Stevens and Baguette, 2008). Overcrowding of an aquatic habitat most likely results in individuals searching for alternatives. To withhold functioning metapopulation dynamics there must be more than a few breeding populations, which are connected to each other to different extents and have access to alternative ponds. Likewise, natural dynamics in for example succession with overgrowth of ponds, and presence and abundance of predators, necessitate a landscape with several potential aquatic habitats within migration distance (Sjögren-Gulve, 1994; Griffiths and Williams, 2000; Jeffries, 2005). It is also important that an adequate disturbance is present in the landscape, creating and renewing ponds continuously. The combination of aquatic and terrestrial habitats constitutes a pond landscape, or “pondscape” (Fig. 3) (Swan and Oldham, 1993; Joly et al., 2001; Malmgren, 2002). In a natural landscape, such dynamic pondscapes might have been created by for example recurring floods, meandering rivers or beaver activity. Even though humans have often caused destruction of natural habitats and removed natural dynamics from landscapes, construction of ponds foremost in agricultural landscapes have probably sometimes replaced and/or complemented natural habitats.

Figure 3. A typical “pondscape” for the great crested newt (courtesy of Per Wedholm).

Different terrestrial environments have different quality and function in the pondscape. Areas that do not function as terrestrial habitat for the great crested newt might still be important as corridors between aquatic and terrestrial habitats. An ideal pondscape for the great crested newt and other pond-breeding amphibians is constituted by several used or potential aquatic habitats. In connection to the aquatic habitats, there must be a sufficient amount of adequate terrestrial habitat. Moreover, the surrounding and interjacent environment should allow for migration between aquatic and terrestrial habitats (Boothby, 1997; Griffiths and Williams, 2000; Langton et al., 2001). It is not clear what makes a pondscape large enough (i.e. number of ponds and area of terrestrial habitat) to support a viable population of great crested newts.

5 Evaluating the habitats of the great crested newt

The aim of this thesis is to analyze what constitutes valuable ecological determinants of great crested newt habitats. I examine physical, chemical and biological characteristics of the aquatic habitat as well as the species´ movements and micro-habitat use in the terrestrial habitat. I also look into landscape characteristics of the terrestrial environment surrounding aquatic habitats. The purpose of the thesis is also to present the results in the perspective of conservation measures and to discuss them in relation to practical examples.

5.1 Study area

The areas where the study was conducted are all located in Örebro County in south-central Sweden (approximately 59^{o}N 15^{o}E). The county covers an area of approximately 9 300 km^2 (Fig. 4). In the northern, southern and western parts of the county the bedrock is mainly granite of the Scandinavian Shield. The elevation here varies between 50 and 400 meters above sea level (in approximately 80 % of the county area) (Fig. 4). The bedrock of the central eastern part of the county is mainly sedimentary and Cambro-Silurian, with sand-, lime- and clay stone. Here, the elevation is between 20 and 100 meters above sea-level (approximately 20 % of the county area). The division between higher and lower elevation areas in the county is sharp and in part consists of escarpments. This sharp division brings a well-defined limit in climate and temperatures. The "*Limes Norrlandicus*", which runs across the central regions of Örebro County, represents the northern distribution limit for many nemoral or hemiboreal species, and the southern limit for many boreal species.

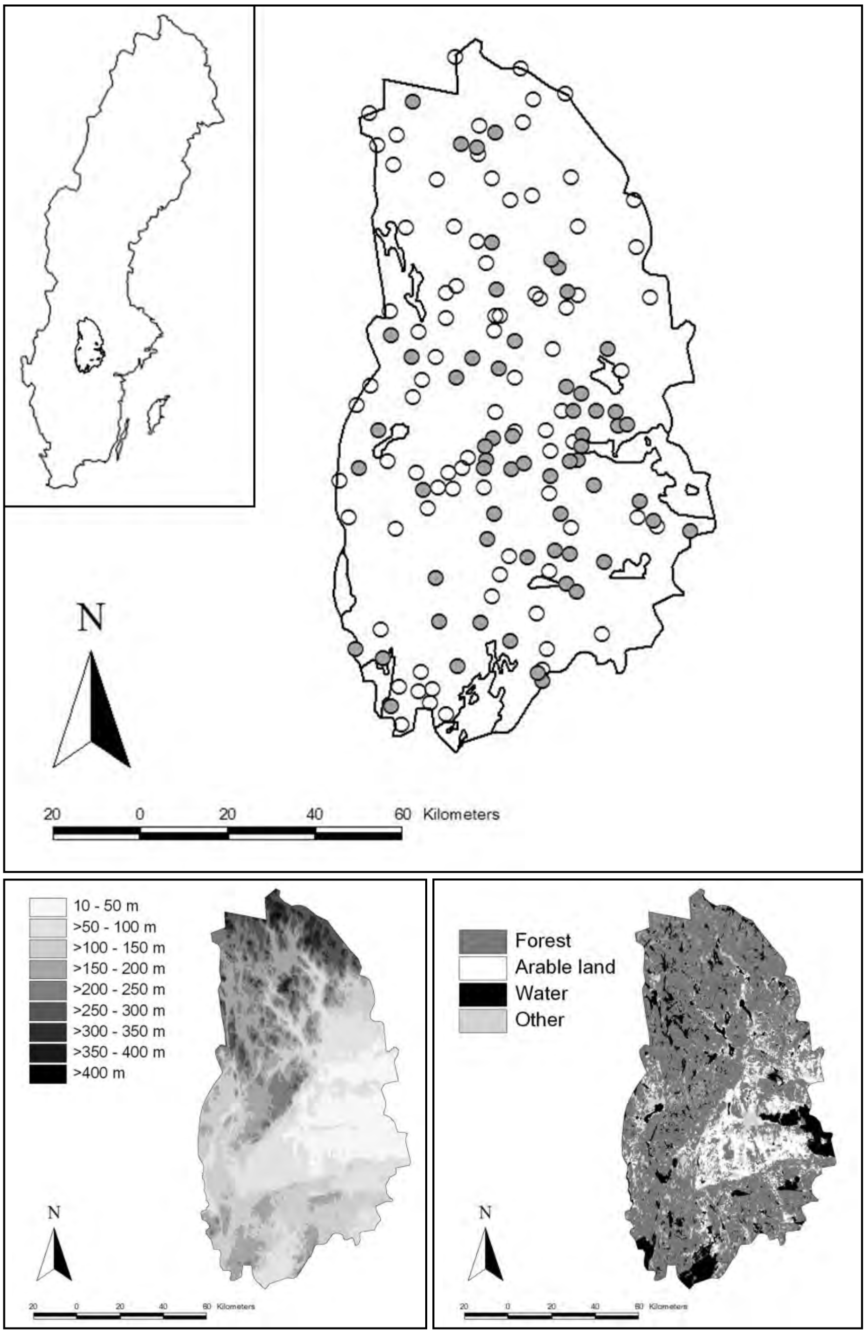

Figure 4. Three maps showing the Örebro County. The uppermost map shows locations of studied ponds with presence (grey circles) and absence (open circles) of great crested newts (the small map in the upper left corner shows the general location of the Örebro County in Sweden). The map at the bottom left shows topography and the map at the bottom right show land categories. © Lantmäteriet, I2011/0032

For example, many hardwood tree species (e.g. *Ulmus glabra, Fraxinus excelsior, Quercus robur, Tilia cordata*) mainly occurs in the lowland and in pockets on slopes elsewhere. Otherwise, the forests of the county are primarily coniferous (*Picea abies, Pinus sylvestris*) with some admixture of deciduous trees (mainly *Populus tremula, Betula pubescens, B. pendula, Alnus glutinosa, Sorbus aucuparia*). The central eastern part is the most densely populated, and the land use is dominated by large-scale agriculture, with fragmented remains of small-scale farmland with natural pastures (Fig. 4). The northern, southern and western parts of the county is less populated and dominated by forests with extensive forestry. Small scale agriculture is also present. The great crested newt is distributed throughout the county, in small-scale agricultural landscapes as well as in areas mainly dominated by mixed or coniferous forests (Fig. 4). The species is also present in more large scale agricultural landscapes, though there are a smaller number of adequate ponds for breeding and a smaller amount of terrestrial habitat. In addition to the great crested newt, there are four amphibian species present in the study area (*Bufo bufo, Rana arvalis, R. temporaria*, and *Lissotriton vulgaris*) and all these species may be found throughout the county.

5.2 Paper I: Newts and pond plant diversity

Observations of the great crested newt suggest that a good quality aquatic habitat for the species should contain a quantity of high-quality food resources, few or no large predators and abundant and varied vegetation. Several other amphibian species, as well as invertebrates using ponds and similar types of aquatic habitats appear to have many demands in common with the great crested newt (Gee et al., 1997; Sahlén and Ekestubbe, 2001; Hartel et al., 2007; Honkanen et al., 2011). This implies that there is a possible indicator ability of the species. In **Paper I**, the composition and quality of the vegetation in the aquatic habitat of the great crested newt was investigated. Specifically, I wanted to know if the number of aquatic plant species was higher in ponds with great crested newts than in ponds without the species.

I analyzed the diversity of macrophytes in paired samples of ponds in a total of five geographically separated sites. Each sample contained one pond with presence of great crested newts and one pond where the species was absent. During the peak of the vegetation period, aquatic macrophytes were sampled by establishing transects across the ponds and by collecting and identifying plants throughout the ponds. The surface vegetation cover was estimated visually as the area covered by emerging plants as a proportion of total pond area. The collected data were analyzed using paired two-sample t-test and Type

II regression analysis (Sokal and Rohlf, 1995). I also performed a Spearman correlation analysis on the relationship between plant diversity and surface vegetation cover to see if these factors correlated with presence and absence of the great crested newt.

In total, I identified 117 plant species accumulated in all ponds studied during the survey. Ponds with and without great crested newts had a cumulative plant species richness of 93 and 68 species, respectively. In general, ponds with great crested newts had a higher mean number of plant species (on average 30.8±5.4) than ponds where the species was absent (on average 21.4±3.4) (paired *t*-test: t=2.35, df=4, P<0.05). The results also implied that the great crested newt prefers ponds with a lower coverage of surface vegetation. However, the difference in vegetation cover between ponds with great crested newts (mean cover 53.0±10.91% SE) and ponds where the species was absent (mean cover 65.6±17.63% SE) was not statistically significant (paired *t*-test: t=1.23, df=4, P>0.05). Plant diversity declined as the amount of pond surface vegetation cover increased, but this tendency was not significant either (Spearman´s correlation test: r=-0.55, P>0.05) (Fig 5).

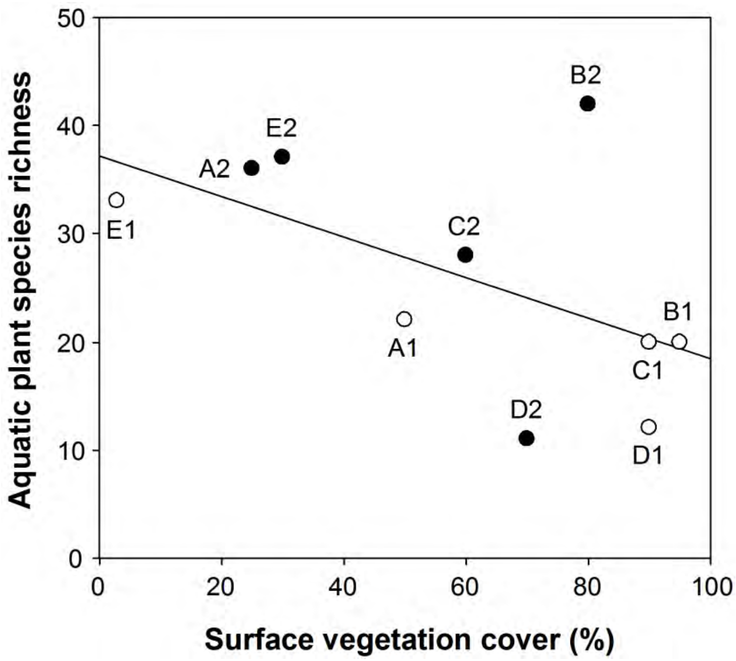

Figure 5. Relationship between aquatic plant species richness and pond vegetation cover in the ten studied ponds. Filled and open circles represent, respectively, ponds where great crested newts were present and absent. Pond designations follow table 1 in **Paper I**.

The results from the study support the hypothesis that high vegetation diversity is an important feature of the great crested newt aquatic habitat. A varied macrophyte flora presents a variety of alternatives for egg laying and as protection for eggs and larvae from predators. Probably, rich and diverse vegetation is also positive for the development of a rich invertebrate fauna (Friday, 1987; Oertli et al., 2002). This secondary effect is likely to have a positive influence on the reproductive success of the great crested newt, as it increases food availability. Ponds and other small lakes and wetlands, that constitute aquatic habitat for the great crested newt, naturally undergo a succession with overgrowth as the end result (Angelibért et al., 2004). When a pond grows older, several colonizing plants tends to decrease in favour for a few dominating macrophyte species that are more competitive in later phases of pond development (Engelhardt and Ritchie, 2001; Engelhardt and Ritchie, 2002; Loreau et al., 2001). As sediments and litter accumulate, the pond becomes more shallow and nutrient rich. Underwater macrophytes are replaced successively by more semi-aquatic plants such as grasses and reeds (Fig. 6) (Angelibért et al., 2004). My results indicate that this plant succession, reinforced and accelerated by high nutrient availability, reduces the quality of the aquatic habitat for the great crested newt with time, and that newts may prefer early and mid phases. As succession progress the pond will overgrow and eventually be totally covered. Consequently, open water will disappear, making the site less favourable for newts in terms of reproduction (Oldham et al., 2000). Thus, for a pondscape to be sustainable from great crested newt perspective over longer periods of time, both landscape dynamics and pond succession is important. Processes that cause recurrent disturbances, creating or re-creating ponds as aquatic habitats for the great crested newts, are therefore of great importance (Semlitsch, 2002; Rannap, 2009).

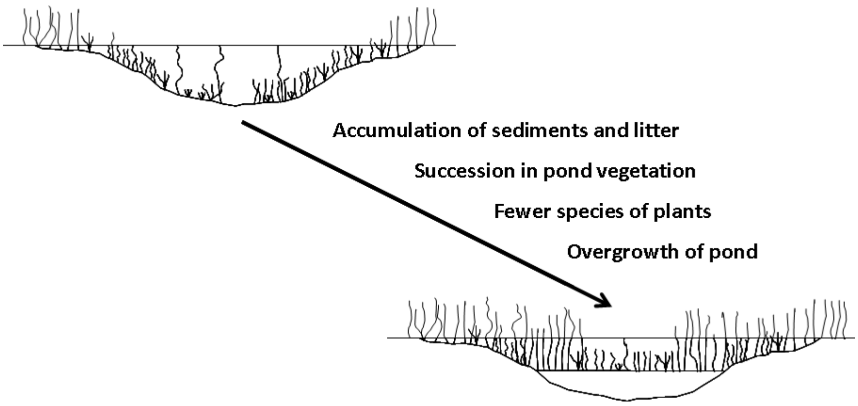

Figure 6. Schematic figure showing succession with overgrowth in ponds, leading to degradation of a great crested newt habitat.

The results confirm the hypothesis that the diversity of aquatic plant species is higher in ponds with great crested newts than in ponds without the species. Vascular plant species richness is not only important for the great crested newt, but also for many other organisms thriving in ponds and other small wetlands (Oertli et al., 2002; Honkanen et al., 2011). In this perspective, the study also supports the idea of using the great crested newt as an indicator or umbrella species for biological diversity of pond species communities.

5.3 Paper II: Pond quality and great crested newts

The chemical status of the aquatic habitat for the great crested newts, as well as the tolerance of especially larvae and eggs to different chemical and physical conditions, have been studied by several researchers (e.g. Cooke and Frazer, 1976; Griffiths and DeWijer, 1994; Thiesmeier and Kupfer, 2000; Skei et al., 2006). For example, eggs and larvae are especially sensitive to the presence of toxic substances. Further, high levels of different nitrogen compounds and low pH can be toxic for amphibians, including the great crested newt, and may cause increased embryonic death, reduced hatchability, and sub-lethal responses (Andrén et al., 1988; Griffiths and De Wijer, 1994; Watt and Oldham, 1995; Ortiz et al., 2004). The importance of water quality parameters to the great crested newt is therefore addressed specifically in **Paper II**.

I compared a number of physical and chemical parameters between ponds without great crested newts, ponds with great crested newts and ponds where the species was successfully reproducing. A cluster of 33 ponds were surveyed for great crested newts using standard methods. Water sampling and temperature measurements were conducted in all ponds on four different occasions during one year. In later analyses, mean values from these four occasions were used for 29 of the surveyed ponds. Eleven parameters of water quality were measured in each pond.

I found significant differences (two-sample t-test) between ponds with and without great crested newts for three of the measured variables: temperatures were higher in ponds with great crested newts (t=3.10, df=27, P<0.05); total phosphorus (t=2.24, df=27, P<0.05) and the phosphate/phosphorus ratio (t=2.49, df=27, P<0.05) levels were higher in ponds where the species was present. Principal components analysis and logistic regression with Akaike´s Information Criteria (AIC) combined, showed that the most important variables distinguishing between ponds with and ponds without great crested newts were nitrogen, phosphorus and temperature (Fig. 7). When comparing ponds without newts, ponds with newts but without reproduction and ponds with reproduction, there was a significant difference among the groups found on a PC-axis which was highly correlated with variables corresponding to nutrients. The group with great crested newts but without reproduction had significantly higher values than ponds without newts (B=2.476, P<0.05) and ponds with reproduction of newts (B=5.400, P<0.05). There were no significant differences between ponds with reproduction and ponds where the great crested newt was absent, in terms of the variables measured in this study.

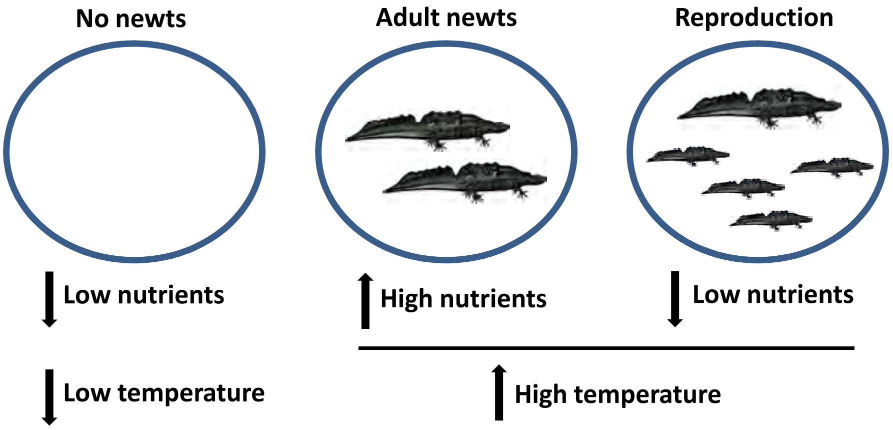

Figure 7. Levels of nutrients (nitrogen and phosphorus) and temperature differed between ponds without newts, ponds with newts and ponds with reproduction. Ponds without newts and with reproduction of newts had lower values of nutrients than ponds where newts were present without reproducing. The two groups with presence of newts, combined, had higher mean temperature than ponds without newts.

The results of the study confirm that there are differences in water quality between ponds, which are of importance for the presence and successful reproduction of the great crested newt. The most obvious differences were observed when comparing levels of nitrogen, phosphorus and temperature, while differences in for example pH, conductivity and alkalinity appeared less important. Possibly the great crested newt has adapted to manage a wide variety of aquatic habitats, with a variation in levels of chemical substances. Of course, noxious levels of any kind would be avoided actively by adults or result in unsuccessful breeding (Watt and Oldham, 1995; Malmgren, 2001; Ortiz et al., 2004; Smith et al., 2006; Griffis-Kyle, 2007). However, when selecting among aquatic habitats, breeding adult newts may prefer environments where there are optimal conditions for egg laying and where survival of eggs and larvae have the highest priority (Malmgren, 2001). For this choice, levels of chemical substances per se may be secondary. More important could be for example good-quality substrate for egg-laying (abundant and varied vegetation, *sensu* **Paper I**), that the pond is free from ice when adults arrive in spring (otherwise they may leave for another pond) and/or adequate overall temperature and high production of prey. The quality of vegetation is to a large extent affected by the levels of nutrients (Engelhardt and Richie, 2001; Loreau et al., 2001; Knutson et al., 2004; Rosset et al., 2010), which could explain the significant differences in levels of nitrogen and phosphorus. Relatively high water temperatures are almost certainly important for egg and larval growth and development. Time of development from egg to larvae to adult newt differs depending on water temperature (Griffiths and De Wijer, 1994; D´Amen et al., 2007). High temperature and sun insolation is not only affecting growth and development of the great crested newt directly, it is also positive for the emergence of abundant aquatic vegetation and for maintaining a plentiful supply of invertebrate food resources (e.g., Werner and Glennemeier, 1999; Oldham et al., 2000; Thiesmeier and Kupfer, 2000; Rosset et al., 2010). Ponds that lack features essential for reproduction may be sufficient enough for foraging and are perhaps visited by moving adults in search for new potential breeding habitat. They may also attract individuals from over-crowded aquatic habitats in the vicinity, but are as such suboptimal habitats for reproduction. If some individuals breed and lay eggs, scarcity of adequate egg laying substrate and protecting vegetation may cause increased predation on eggs and larvae and/or exposure to lethal radiation (Miaud, 1994; Griffiths et al., 1996; Oldham et al., 2000; Marco et al., 2001). In this sense, one may divide ponds used by great crested newts into either “nesting sites”, sufficient for reproduction, or “resting sites”, where newts may stay for foraging or other purposes but without reproducing (Malmgren, 2001). Nesting sites are relative productive ponds with high temperatures, abundant vegetation and high species richness, where most of the nutrients are bound to living organisms. Resting sites may be ponds with lower productivity and a high amount of dissolved nutrients, which would explain the pattern found in the study.

5.4 Paper III: Movements of great crested newts

Like many amphibians, the great crested newt has a biphasic life cycle, with seasonal movements between their aquatic habitat (usually a pond) and terrestrial habitat. Nevertheless, little is known about the terrestrial phase. Since conducting terrestrial studies on social interactions among newts in the field is difficult, most studies on the great crested newt and other pond-breeding amphibians have been conducted in their aquatic habitat where they are comparatively easy to find. Furthermore, most conservation measures for the species is focused on breeding ponds, leaving terrestrial elements of its habitats neglected. However, to achieve favourable conservation status of a population and of the species, not only the aquatic habitat of the species should be considered.

To constitute a sufficient terrestrial habitat for the great crested newt an environment should provide foraging opportunities, as well as protection from desiccation and predators, during post-breeding activities and juvenile dispersal (Griffiths, 1996; Thiesmeier and Kupfer, 2000; Langton et al., 2001; Malmgren et al. 2007). The habitat must also contain shelters for refuge during more extreme weather conditions, and allow for hibernation during winter. To delineate the terrestrial habitat of the great crested newt one must obtain knowledge on movement patterns and migration distances on land. It is also crucial to learn more about micro-habitat use in the terrestrial environment. The purpose of **Paper III** is therefore to explore how great crested newts move in their terrestrial habitats, when leaving their aquatic habitat after breeding. I also wanted to find out if the species preferred certain structures as day shelters or when moving through their terrestrial habitat. The study was performed in 2001, as one of the first telemetric studies on great crested newts.

I used radio transmitters to mark and follow the movements of great crested newts on land on two different locations (Lillsjön and Äspsätter) west of the city of Örebro in south-central Sweden. Radio-tracking is a monitoring technique which is suitable for collecting data on migration patterns and terrestrial habitat use of newts, as searching for newts in their terrestrial habitat may otherwise be destructive due to their cryptical way of living. In total, 20 (Lillsjön) and 9 (Äspsätter) individuals were marked with transmitters implanted in the abdomen of the newts. Implantation was chosen prior to external transmitters to avoid injuries on the animals and to prevent transmitters from falling off (Jehle and Arntzen, 2000). The batteries of the transmitters allowed for 3-5 weeks of tracking. Tracking was mainly conducted during night, when the newts were most active, and all individuals were tracked at least once every day. Shelter use and a number of terrestrial parameters were recorded on all locations where the individuals were found during tracking. The locations were divided into "short stays", where individuals stayed for a shorter period than 72 hours, and "long stays" where they stayed for more than 72 hours. The locations where they stayed for a longer period were considered as sites preferred by the great crested newt.

All individuals but 4 left the release-point on the night of release and moved between 9 and 132 m away from the pond. Most of the marked individuals made their largest single movement during the first 24 hours after release. Maximum single movement of an individual within 24 hours was 132 m at Lillsjön and 47 m at Äspsätter. The longest total migration distance by one individual was 293 m at Lillsjön and 94 m at Äspsätter. The longest net migrated distance was 207 m and 75 m respectively. The minimum convex polygon covered an area of 3.9 ha at Lillsjön (combined, n=19) and 0.6 ha at Äspsätter (combined, n=9). The results indicate a preference for structures such as underground cavities among tree roots, rotting tree stumps and dead logs (Fig. 8). Such elements and structures could be used to improve an otherwise insufficient terrestrial environment as terrestrial habitat for the great crested newt. However, the tracked newts were often found in leaf litter or in the surface vegetation when staying for shorter periods, for example when moving between shelters.

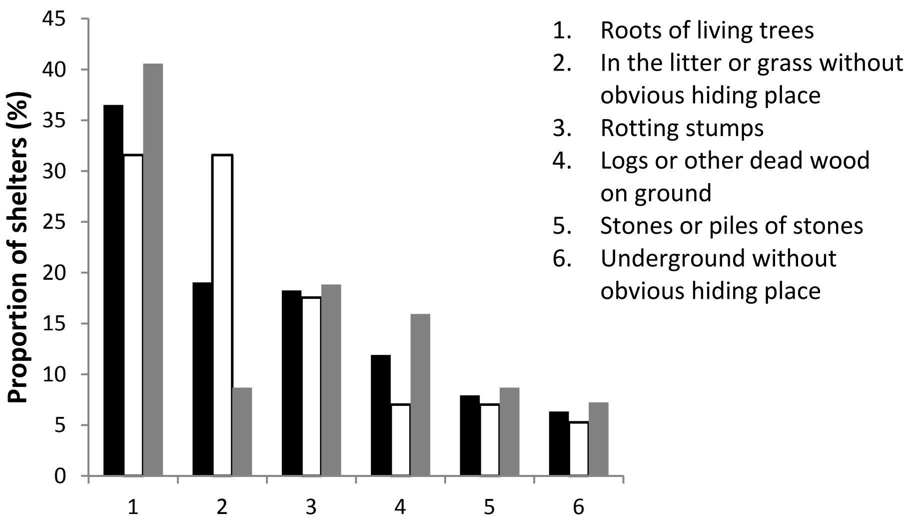

Figure 8. Shelters used by great crested newts marked with radio-transmitters in two different habitats in south-central Sweden. Black bars shows proportion of total number of shelters used by the marked individuals at the two ponds combined (n=126); white bars include shelters used for less than 72 hours (n=57); grey bars include shelters used for more than 72 hours (n=69).

The distances and areas covered by the tracked newts in this study agree with results from similar studies performed on the great crested newt and other species of the same genera, suggesting that the terrestrial area mainly used as habitat lies within approximately 200 m from a breeding pond (Cooke and Frazer, 1976; Jehle, 2000; Jehle and Arntzen, 2000; Thiesmeier and Kupfer, 2000; Schabetsberger et al., 2004). Short migration distances should be preferred, when possible, to allow for earlier arrival at the breeding site in spring. This is especially important in the study area, considering the short breeding season at the northern distribution limit of the species. Possibly, migration in the terrestrial environment is directed towards preferred micro-habitats and shelters that have proven to be of good quality (for example providing frost safe hibernation sites) (Malmgren, 2002).

Almost all movements took place within forested areas, although a large part of the surroundings of the ponds consisted of fields and other open land (see also Malmgren, 2001; Malmgren, 2002). As has also been demonstrated in other studies, this indicates that great crested newts avoid fields and similar open environments and prefer woodland or semi-natural meadows and pastures when on land (Jehle and Arntzen, 2000; Joly et al., 2001; **Paper IV**). However, there are probably structural differences within the forest and the availability of micro-habitats and suitable shelters may vary substantially and could in some areas be a limited resource.

The relatively short migration distances shown in this and other studies demonstrate the importance of connectivity in landscapes or pondscapes. When delineating reserves or management areas for great crested newts, it is of vital importance to consider the combination of aquatic and terrestrial habitats, and to delimit sufficient amount of adequate terrestrial habitat in the near surroundings of one or several potential breeding ponds. Delineation of terrestrial reserves should be made according to preferred habitats rather than constructing a circular reserve around a breeding habitat (see also Dodd and Cade, 1998; Schabetsberger et al., 2004).

5.5 Paper IV: Landscape composition and newt occurrence

Amphibians in general are much dependent on the environment surrounding their breeding habitat, due to their biphasic life cycle and their restricted dispersal ability (Bowne and Bowers, 2004; Becker et al., 2009; Popescu and Hunter, 2011). In pondscapes inhabited by great crested newts and several other amphibian species, the aquatic and terrestrial habitats constitute equally important landscape elements. Consequently, the amount and quality of both elements must be sufficient and the habitats have to be adjoining or interconnected in some way to make movements between them possible. Also, different types of land use and vegetation are probably important on different spatial scales and distances from an aquatic habitat (Ficetola et al., 2009). When planning for conservation measures, a landscape approach is therefore essential. The land cover and land use pattern of the landscape surrounding aquatic habitats of the great crested newt may mirror a preferred constitution of its terrestrial habitat at different spatial scales. The purpose of **Paper IV** was to examine differences in structure and composition of landscapes surrounding ponds with and without great crested newts.

In order to explain the use of ponds as aquatic habitats, I related presence and absence to 31 variables in a total of 143 areas (61 with great crested newts and 82 without) throughout Örebro County. I used two important pond variables (presence of predators and size of ponds), one regional variable (altitude), and 15 variables describing the landscape surrounding potential breeding ponds (proportions of 13 land cover categories and distance to forest and deciduous forest). Landscape variables were measured and analyzed at two different scales, within a radius of 100 m (local scale) and 500 m (landscape scale) surrounding the ponds. I used principal component analysis (PCA) and logistic regression analysis with Akaike´s Information Criteria (AIC) to distinguish variables important for the distribution of great crested newts.

My results suggest that features such as landscape composition and the amount of available terrestrial habitat may indeed serve to predict which ponds are used as aquatic habitat for the great crested newt. Breeding ponds tended to be located closer to forests and especially deciduous forests than did ponds without great crested newts. Furthermore, a high amount of deciduous forest and pastures was positive for the presence of great crested newts. On the other hand, coniferous forest and mire appeared to have a negative effect on the habitat quality for the species. I could not detect any apparent differences between different scales, but for example deciduous forest was important on both local and landscape scales. These findings confirm the assumption that deciduous forest and pastures are preferably used as terrestrial habitat by the great crested newt and that coniferous forest is suboptimal as terrestrial habitat for the species (Griffiths, 1996; Latham and Oldham, 1996; Jehle and Arntzen, 2000; Thiesmeier and Kupfer, 2000; Malmgren 2007).

When the results from **Papers III** and **IV** are combined, it becomes apparent how crucial it is to lift the focus from only recognizing the aquatic habitat as important for the great crested newt. Instead, it must be stressed that the combination of aquatic and terrestrial habitats, and the composition of the pondscape, is the best frame used when considering both the ecology and the appropriate conservation measures for this species. The results imply that management of the great crested newt should to a greater extent include the terrestrial habitat, with special attention given to older, deciduous-rich forest in the vicinity of breeding ponds. Heterogeneous and less intensively managed areas, with a relatively large quantity of deciduous forest appear to be preferred by the great crested newt as well as by other northern European amphibians, as well as a number of other species connected to ponds and small wetlands (Møller and Rørdam, 1985; Latham and Oldham, 1996; Davies et al., 2004; Johansson et al., 2005; Bloechl et al., 2010). However, one should keep in mind that there are several other parameters, both biological and physical, influencing the habitat selection of the great crested newt that are not included in this study. Apart from several aquatic habitat parameters, the structure and relative position of different types of land cover may be important. Also, pond connectivity is important for withholding long-term viability of a population and for supporting the metapopulation dynamics (Karlsson et al., 2007; Ribeiro et al, 2011). The combination of high quality aquatic and terrestrial habitats is the key to maintaining large, viable populations. It is of vital importance to coordinate the planning of aquatic and terrestrial habitats, for example when making priorities for construction and restoration of breeding ponds for newts and other amphibians. Even if the breeding habitats are not destroyed, amphibian populations may be negatively affected by for example agricultural intensification or urban development in the surrounding landscape (Curado et al., 2011). Studies on amphibian populations should consider multiple factors that potentially may affect distribution and survival in different habitats. Nevertheless, I argue that the terrestrial habitat use of the great crested newt may reflect that of other semi-aquatic organisms. The planning and management for this species may therefore benefit a large number of species dependent on functional pondscapes.

5.6 Paper V: Translocation of a great crested newt population

A large number of great crested newt habitats have disappeared or deteriorated during the last century (Beebee and Griffiths, 2000; Edgar and Bird, 2006; Malmgren, 2007). Such habitat destruction, has led to fragmentation of populations and other negative effects that have caused the number of great crested newt populations to decrease. Due to this reduction, the species is now threatened and protected in its entire European distribution range (Temple and Cox, 2009). Current legislation conveys that not only the species itself, but also its habitats, may not be disturbed in any way without permission. Nevertheless, the protection of the species together with an improved knowledge on great crested newt distribution and localities has brought an increased awareness of conflicts between newts and human exploitation projects (Langton et al., 2001; Edgar and Bird, 2006; Malmgren, 2007). The strong protection of the species often prevents exploitation and destruction of habitats, but during recent years a common solution has been to translocate animals to alternative habitats as a compensation for habitat destruction (Edgar and Griffiths, 2004; Edgar et al., 2005). In **Paper V** I therefore describe and discuss an interesting case of translocation of great crested newts carried out close to the city of Örebro in 2007 and 2008.

The translocation project in Örebro was started due to a planned re-fill and development in an old gravel pit containing a great crested newt breeding habitat. The population in question had already been subjected to a translocation, as there were re-fill plans already in 1989. A large part of the population was then moved to a newly constructed pond in a protected area in the outskirts of Örebro. Due to this earlier translocation, the degradation of the aquatic habitat following the translocation and the isolated location in relation to other populations of great crested newts, the municipality got a permit to re-fill the gravel pit and destroy the newt habitat in 2007. As compensation, they were enjoined to translocate any remaining individuals of the population and the entire amphibian community in the pond to a newly constructed pond located approximately 10 km from the original habitat. To catch and move as many individuals as possible, a drift fence with pitfall traps was put up surrounding the aquatic habitat during two years. The fence was put up in late April, when the newts started to migrate towards their breeding habitat after hibernating in their terrestrial habitat. At the receiving area, all newts and other amphibians were released in the same pond. The result of the translocation was monitored during 2008 and 2009, using a drift fence surrounding the pond where the newts were released.

In the spring and early summer of 2007, a total of 730 great crested newts had been caught and translocated from the original habitat in Marieberg (Fig. 9). An additional 59 great crested newts were caught and translocated during spring and early summer of 2008. The translocated population in the receiving area (Vattenparken) was monitored in 2008 and 2009. During the spring migration from April to June 2008, 49 great crested newts were caught when migrating from their terrestrial habitat towards the pond. This corresponds to 6.7 % of the population that was translocated in 2007 (in total 730 individuals). Great crested newts were also found to have migrated to two other ponds in the vicinity of the receiving pond. From April to June 2009, 224 great crested newts were caught moving from their terrestrial habitat towards the three ponds that were confirmed to hold great crested newts in the Vattenparken area in 2008. Of those, 181 newts migrated towards the pond receiving the translocated individuals in 2007. The visual survey of all ponds in the surrounding area in 2009 showed that adult great crested newts were present in an additional four ponds apart from the receiving pond. Reproduction of great crested newts could be confirmed in the receiving pond in both 2007 and 2008, as eggs and larvae were found. However, in 2009, no reproduction of great crested newts could be confirmed after dip-netting in the three fenced ponds, including the receiving pond.

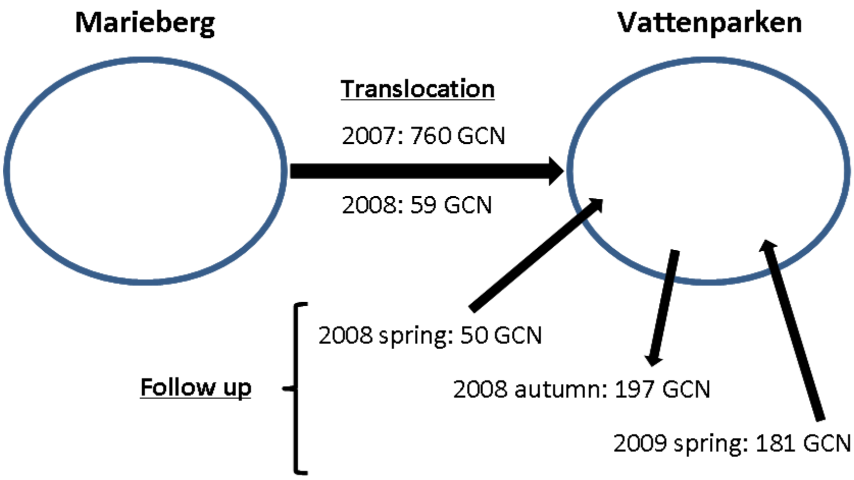

Figure 9. The different stages of a translocation and the subsequent monitoring of a population of great crested newts (GCN). The population was translocated from its original habitat in Marieberg during two years (2007 and 2008) and surveyed during the two consecutive years at the receiving pond in Vattenparken.

The number of caught great crested newts at the source pond in Marieberg was much larger than anyone had expected before the translocation and the population size was substantially underestimated. Both aquatic and terrestrial habitats were apparently sufficient for breeding and survival, and the population had time to recover after the first translocation in 1990. This exemplifies how difficult it is to determine size and conservation value of a great crested newt population based on habitat appearance and without thorough initial investigations. Since great crested newts may live for a long time without successful breeding (Dolmen, 1982; Thiesmeier and Kupfer, 2000), a significant part of a great crested newt population may abide for several years even in a sub-optimal habitat. Therefore, prior to a massive operation such as a translocation a thorough survey of the population and its prerequisites in the original habitat should be performed at least two years prior to effectuation. Furthermore, before a translocation is performed, it should be confirmed that the receiving area fulfil necessary habitat criteria. In contrast to many other translocation projects, in the case of semi-aquatic organisms like the great crested newt, both aquatic and terrestrial habitat must be accounted for and not only the quality of the receiving pond should be considered.

Translocation of a population may be a tool for companies and authorities to get around the protection of the species and its habitats. However, a large part of the translocated population in Örebro (approximately 90 %) disappeared from the receiving area, which shows that such a project may be very harmful to a population of great crested newts. The monitoring in

Vattenparken in the summer of 2008 indicates that part of the translocated population was established in their new habitat and that reproduction occurred. However, in 2009 no breeding could be confirmed. The reasons for this failure are unclear and the pond in Vattenparken ought to be monitored continuously for at least another seven years, to be able to assess if the translocation project as a whole has failed or succeeded. Long-term monitoring is necessary to distinguish if a translocation project is a success with respect to site sustainability and population size (IUCN, 1998). This is particularly important when working with a long-lived species such as the great crested newt.

Reviews show that a majority of performed and reported translocations appear to be unsuccessful (Dodd and Seigel, 1991; Seigel and Dodd, 2002; Germano and Bishop, 2009). Especially translocations aimed to solve human-animal conflicts run the risk of failure (Fischer and Lindenmayer, 2000; Germano and Bishop, 2009). Most translocation projects have been performed without being properly monitored and without the results being published (Dodd and Seigel, 1991; Oldham and Humphries, 2000; Edgar et al. 2005; Germano and Bishop, 2009). This is problematic because there is a great need to share such results and learn from mistakes and success to make translocations and other conservation measures efficient. We also need further evidence to be able to consider if translocations is a good option as a compensation for habitat exploitation. I argue that translocation should never be a first choice to make human development possible. One should always try to preserve a population in its original habitat (*in situ*) as long as it is possible. To establish new great crested newt populations in for example constructed habitats, translocation of a part of a natural population could be an alternative. However, the use of translocation as an alternative conservation strategy may only be decided after considering the probability of success in the specific case.

6 Implications for management and conservation

The great crested newt is one of few amphibian species adapted to the Scandinavian environment and climate. Together with other amphibian species in its distribution range, it is decreasing due to habitat destruction and habitat fragmentation after intensified agriculture and forestry. Out of the five amphibian species present within the study area, the great crested newt is probably the most threatened and vulnerable (Malmgren, 2007). The same is valid throughout most of the distribution area of the species in Sweden. The preservation of such a species is therefore of uttermost importance and a national responsibility that requires both the conservation and restoration of existing habitat and creation of new habitat.

The results of the studies presented in this thesis demonstrate that several variables at different levels and scales influence both habitat quality and habitat selection of the great crested newt. For example, there are chemical, physical and biological determinants on both local and landscape scales. The aquatic habitat is not only affected by factors in the water itself, but also by the surrounding landscape **-** for example by the amount and type of forest in the vicinity of the pond, bedrock and soils of the surrounding landscape. Furthermore, the aquatic habitat and the surrounding landscape, including the terrestrial habitat, are often shaped by different kinds of human land use that may affect the habitats both positively and negatively. To function as a sufficient terrestrial habitat for the great crested newt, good habitat quality *per se* is not enough if the area is too small or if the distance from potential breeding habitats is too large. Therefore, the connectivity of the landscape is also imperative. **Papers I-IV** describe the habitats of the great crested newt from different perspectives, on different scales and using different variables. I am thereby not diminishing the role of any other biotic (e.g. predation, competition or dispersal behaviour) or abiotic (e.g. landscape permeability or pond characteristics) factors also recognized as drivers in the colonization of ponds by amphibians in general and of the great crested newt (e.g. Cooke and Frazer, 1976; Baker and Halliday, 1999; Kupfer and Kneitz, 2000; Thiesmeier and Kupfer, 2000; Lesbarrerés et al., 2010).

The findings presented in this thesis should be taken under consideration in conservation measures for the great crested newt and especially in the management of ponds and other small wetlands in the distribution range of the species. When constructing new ponds it is essential to analyze the surrounding landscape, not only regarded as terrestrial habitat for the great crested newt but also in terms of its influence on the aquatic habitat (Davies et al., 2004; Hamer and McDonnell, 2008). For example, while ponds constructed mainly for nutrient retention should be placed where there are high influxes of nutrients and therefore a high level of nutrient uptake (Brönmark and Hansson, 1998; Brönmark and Hansson, 2002), it is often important to avoid high nutrient levels when constructing ponds for enhancing amphibian diversity in the landscape (Hamer et al., 2004; Kadoya et al., 2011). **Paper II** indicates this, where newts were shown to avoid ponds with high nutrient levels when selecting breeding habitat. High levels of nutrients might be harmful *per se* and additionally accelerate over-growth and succession of the pond. Over-growth often means a transformation of pond vegetation, from a species-rich community with a diverse flora of macrophytes to a species-poor community dominated by plants merging over the surface (Engelhardt and Ritchie, 2001; Engelhardt and Ritchie, 2002; Loreau et al., 2001; Angelibert et al., 2004). As discussed earlier and in **Paper I**, this process deteriorates the quality of the pond as a great crested newt habitat, and for the ecosystem it is indicative of.

Even if there are no unnaturally high levels of nutrients, all ponds will eventually overgrow (Gee et al., 1997; Boothby, 2003). This natural or anthropogenically driven succession may be stopped and turned back by recurring mechanical clearing of ponds, and by low-intensity grazing. However, as over-growth is a natural process there are many species of diverse genera that are adapted to different stages in the succession (Gee et al., 1997). To avoid disturbing amphibian populations and other organisms, and as there often is a lack of ponds in the landscape, a better alternative to restoration is often to create new ponds in the vicinity of overgrown ponds. If restoring a pond, an alternative to clearing the whole surface may be to save vegetation in parts of the pond. This will be less harmful to the flora and fauna of the pond and will speed up the colonization by plants and invertebrates.

The closest surroundings of a pond might also be subject to over-growth, due to for example removal of grazing stock. This leads to the invasion of taller herbs, bushes and eventually trees, causes shading to the pond and increased amounts of leaf-litter and nutrient additions. Shading, especially in the south sector of the pond, causes lower temperatures and reduced pond vegetation, while leaf-litter may cause increased levels of nutrients and a lack in oxygen (Gee et al., 1997; Skelly et al., 2002; Thurgate and Pechmann, 2007). **Papers I** and **II** indicate the importance of diverse vegetation and high temperature for successful breeding of great crested newts. Consequently, it may also be important to take the terrestrial vegetation within approximately 20 meters of a pond into consideration when working with conservation measures in the aquatic habitat of the species (Sztatecsny et al., 2004).

The radio-transmitter study in **Paper III** demonstrates the importance of certain structures and micro-habitats in the terrestrial habitat of the great crested newt. Structures such as dead wood and abundant leaf litter are primarily restricted to habitats that are rare in the human influenced landscapes of today, like old-growth forest and deciduous forest (Nilsson et al., 2002; Mikusiński et al 2003; Bobiek et al., 2005). However, as a conservation measure, the availability of such structures may be enhanced in areas where the quality of the terrestrial habitat would otherwise be deficient. By supplying forest floors with litter from e.g. surrounding parks and lawns or with logs and other coarse woody debris, new micro-habitats will be created.

As shown in **Paper III**, the great crested newt prefers to use the area close to the aquatic habitat as terrestrial habitat. This tendency has also been pointed out in similar studies on the species (Dolmen, 1982; Latham and Oldham, 1996; Baker and Halliday, 1999; Oldham and Humphries, 2000; Jehle, 2000; Jehle and Arntzen, 2000; Malmgren, 2002). Movements on land expose a newt individual for potential risks, like predators and desiccation, especially since the great crested newt moves rather slowly while on land. Consequently, they ought to prefer habitats close to the breeding pond if they are available. Thus, habitat reinforcement measures in the terrestrial habitat ought to be most advantageous within approximately 200 m from a breeding pond or a potential aquatic habitat. However, to allow for changes in the surrounding landscape and to render migration between ponds and populations possible, it is necessary to have a more large scale approach.

In **Paper IV**, I investigated the terrestrial habitat surrounding great crested newt aquatic habitats on two different scales. When working with conservation of great crested newts and other pond-living organisms, it is important to consider the surrounding landscape not only as a terrestrial habitat but also as a mean for transportation between ponds and habitats. How large areas a great crested newt population utilizes depends on the quality of the terrestrial habitat and if the connectivity of the surrounding landscape allows for individuals to migrate. Landscape connectivity and, specifically, pond connectivity is important for the long term persistence of populations with metapopulation dynamics, since it may buffer the stochastic events to which ponds are prone (Marsh and Trenham, 2001; Smith and Green, 2005; Griffiths et al., 2010; Semlitsch, 2010). To sustain viable populations of the great crested newt, there need to be a mosaic of aquatic habitats of different types and succession stages and abundant terrestrial habitat of high quality, with interconnecting corridors and within migration distance, in a pondscape (Swan and Oldham, 1993; Jehle, 2000; Joly et al., 2001; Langton et al., 2001; Malmgren 2002).

Paper V describes a conflict between human land use and great crested newts. A translocation project was performed due to exploitation demands, strong legislation protecting the great crested newt and lacking knowledge in estimating habitat quality. Unfortunately, the project was performed with a time limit, was underfunded and several important elements were left out or overlooked. For example, no initial survey of the population was made prior to implementation, which led to a substantial underestimation of the population size. If a survey had been performed, the population would probably have been preserved in its original habitat. The strong legislation protecting the species and its habitat demands very strong economical or societal motives before destroying a population (Artskyddsförordningen 2007:845). However, sometimes there is no option to habitat destruction and then translocation might be an alternative to make at least part of the population survive and not to decrease the total number of populations in a region. Consequently, there is urgent need to learn how to perform such projects without causing too much damage to the population in question or to the total great crested newt population. It is of utmost importance to follow, describe and publish the results from such examples, to be able to learn from cases and to avoid doing the same mistakes over and over (Dodd and Seigel, 1991). Also, when performing a translocation it is important not to only take the aquatic habitat into consideration. To be sustainable, the receiving area must contain breeding habitat, alternative aquatic habitats, terrestrial habitat and a sufficient degree of connectivity. With this in mind, translocations should only be considered when there are no alternatives to *in situ* preservation. When translocations are deemed necessary, for example if the original habitat has already taken damage, a dedicated long term monitoring regime should be established and sufficient funding should be assigned to the project for its entirety. The need for documentation and appropriate methods also need to be established. To conclude, translocation projects should not be taken lightly. There is also no one method that is appropriate for all such projects, as both the habitat and the life style of the great crested newt are highly complex. Therefore, there is no standard solution to be applied. Each case must be taken into account with a unique approach.

The aquatic habitat of the great crested newt often contains a multitude of life. Ponds and small lakes and wetlands are among the most important for the diversity of aquatic organisms and the presence of a variety of ponds and wetlands adds important features in a heterogeneous landscape (Friday, 1987; Gibbs, 1993; Semlitsch and Bodie, 1998; Williams et al., 2003; Briers and Biggs, 2005; Oertli et al., 2005; Søndergaard et al., 2005). The results from **Paper I** demonstrate that ponds with presence of great crested newts have a higher number of aquatic plant species than ponds where the great crested newt is absent. This implies that presence of great crested newts is a good indicator for high species diversity of plants in ponds and small wetlands. The aquatic environment preferred by the great crested newt contains a large variety of structures and vegetation that constitute egg laying substrate and protection. This variation probably incorporates a large diversity among plants and animals. The same may most likely be applied to the terrestrial habitat of the species, as the great crested newt seems to prefer environments with a high heterogeneity in structures and substrates in the field and ground level (Jehle, 2000; Jehle and Arntzen, 2000; Joly et al., 2001) which is also indicated by **Paper III**. Even the relatively small area enclosed by a 200 m buffer zone surrounding a great crested newt breeding pond may contain valuable flora and fauna (e.g. Götmark and Thorell, 2003), which further motivates the protection of such areas. The specific demands of high quality habitat propose that the great crested newt is a valid indicator or umbrella species for several plant and animal communities and for a heterogeneous and sustainable pondscape (Simberloff, 1998; Baker and Halliday, 1999; Caro and O´Doherty, 1999; Jehle, 2000; Roberge and Angelstam, 2004). In particular, species that demand ponds and wetlands in some part of its lifecycle will probably fall under the protective shade of the great crested newt umbrella. However, it is utterly important that survey and monitoring schemes of great crested newts not only indicate presence or absence of adults, but also observations of reproductive success. It appears that the great crested newt may occur in aquatic habitats with different quality depending on purpose of use (**Paper II**). Especially when selecting breeding habitat, they are certainly more selective. Furthermore, as adult newts may grow fairly old and can remain in a poor-quality landscape for some time, presence of adult newts alone is not a valid sign of a functional pondscape (as indicated by the habitat of the translocated population in **Paper V**). To preserve and restore pond-breeding amphibian populations and to provide a suitable pondscape, there must be appropriate levels of habitat succession, good water quality, absence of predatory fish, availability of terrestrial habitat, and connectivity to surrounding populations. A dynamic pondscape containing a multitude of used or potential aquatic habitats with a natural succession may allow for fish-based and newt-based ecosystems to co-exist on a landscape level. To secure the long-term survival of great crested newts and other amphibians it is necessary to consider a scale large enough to secure population survival and to maintain metapopulations on a landscape scale.

The public opinion on the protection of the great crested newt and its environments is most often positive. It is a charming and attractive species that lead a mysterious life in hidden places, and it is very popular among children and young adults if they learn to know it. It is probably easier to attract attention to the great crested newt than to less eye-catching creatures that hide in the vegetation or mud of a pond, like mayfly nymphs, water flees or leeches. Beautiful flying dragonflies or flowering plants might be attractive, but many times difficult to catch or demonstrate and it is often complicated to distinguish different species. The assumption that the great crested newt may be a good indicator, umbrella and/or flagship species for a large biological diversity, makes it valuable as a motive and symbol for creating and restoring ponds and pondscapes.

7 The need for further research

As the great crested newt is unfamiliar to many people and leads an obscure life, its distribution and habitat selection has remained unknown for a long time. Early studies have mostly been directed towards systematics, morphology/physiology and reproductive biology of the species (Griffiths, 1996; Thiesmeier and Kupfer, 2000). However, a number of more recent studies have been made to outline and describe the habitats and landscapes of the great crested newt. As have been mentioned above, the aquatic habitat is the most well known whereas the terrestrial habitat has been less acknowledged. It is also important to raise the question of habitat preference to the landscape scale, especially in conservation issues.

Future studies are recommended to continue the research on pollutants and diseases, not only concerning the great crested newt but for the amphibian group as a whole. Negative effects of for example different nitrogen compounds or low levels of pH have often been detected and investigated separately and in laboratory environments. Their effects in natural environments, combined with a multitude of other chemical, physical and biological variables have been researched to a smaller extent. In natural ecosystems different organisms are affected to different extent. Nevertheless, a negative effect on one species may convey cascade effects that act negatively on organisms in other parts of the system. It may be difficult to trace the cause of such cascades in natural systems; however, it is of utmost importance to consider this issue when trying to outline actual effects and thresholds of for example different compounds and substances. Future research should study different physical, chemical and biological variables together, to try to find out their combined and relative importance in shaping a sufficient aquatic habitat.

As great crested newts spend most of their lives in a terrestrial environment, it is crucial to delimit not only the aquatic part of their habitat. As seen in **Paper III**, small and light radio-transmitters make it possible to follow individual newts when moving in a terrestrial environment without being destructive (Jehle, 2000; Schabetsberger et al., 2004). More similar studies need to be performed, to find out in what environments the newts move, where they stay for extended periods of time and if certain environments are avoided. It is also important to register which microhabitats are preferred. This is of particular interest when trying to construct, restore or reinforce terrestrial habitats in the conservation of the great crested newt. Terrestrial habitat use may vary between different parts of the distribution range of the species, which makes it important to research in both southern and northern habitats. The relative importance of both the microhabitat and the terrestrial habitat at a larger scale has not been investigated in detail. Possibly, efficient microhabitats may be created in otherwise inhospitable environments such as for example parks, industrial areas and other built-up areas, or in environments with short continuity and in that way compensate for any lack in natural microhabitats (Langton et al., 2001). Radio-transmitters also aid in outlining movement patterns of great crested newts, for example concerning through which environments they move, how they move to find preferred terrestrial environments and how far they move. Such observations will provide valuable information in the construction, shaping and placement of ponds and pondscapes.

Radio-transmitters are associated with relatively high costs and possible harmful injuries on newts. Instead, analyses of the surroundings of aquatic habitats may reveal proportions of different environments and thresholds adequate for the great crested newt to be present and/or reproducing successfully in a landscape. It is important to investigate terrestrial habitat constitution throughout the distribution range of the species and in different landscape types. **Paper IV** is one of few such studies performed in Scandinavia and it is important to continue this research.

In this thesis I have raised the concept of the great crested newt as a potential indicator of biological diversity in ponds and in the pondscape. To confirm such an assumption, further studies of correlations and co-occurrences with other species groups and ecosystems are necessary, as well as studies of the natural dynamics of a pondscape and of great crested newt metapopulations (Simberloff, 1998; Caro and O´Doherty, 1999; Jeffries, 2005). For understanding more about the ecology and appropriate conservation of this species and its ecosystems, I would therefore recommend that the pondscape frame is very fruitful for future researchers to bear in focus.

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