DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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Impacts of habitat loss and restoration on amphibian populations

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following papers, in the text referred to by their Roman numerals. The papers are reprinted by the kind permission of the publishers.

I Rannap, R., Lõhmus, A., Jakobson, K., 2007. Consequences of coastal meadow degradation: the case of the natterjack toad (*Bufo calamita*) in Estonia. – Wetlands 27, 390–398.

II Rannap, R., Lõhmus, A., Tammaru, T., Briggs, L., de Vries, W., Pappel, P., Bibelriether, F. Northern populations of the natterjack toad (*Bufo calamita*) select specific breeding habitats to develop quickly. – Submitted manuscript.

III Rannap, R., Lõhmus, A., Briggs, L., 2009. Niche position, but not niche breadth, differs in two coexisting amphibians having contrasting trends in Europe. – Diversity and Distributions 15, 692–700.

IV Rannap, R., Lõhmus, A., Briggs, L., 2009. Restoring ponds for amphibians: A success story. – Hydrobiologia 634, 87–95.

The contributions of the authors of the papers were as follows:

	I	**II**	**III**	**IV**
Original idea	RR	RR, AL, LB	RR, LB, AL	RR
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ABBREVIATIONS

GIS	geographic information system
LPA	Landscape Protected Area
GLM	general linear model
ANOVA	analysis of variance

1. INTRODUCTION

Large losses in biodiversity are currently being documented around the world in almost all classes of plants and animals (Lawton and May 1995). Moreover, the rate of extinction is greater than any known in the last 100,000 years (Wilson 1992). Among higher taxa, amphibian losses appear to be particularly severe (Blaustein et al. 1994, Houlahan et al. 2000) with 33% of the approximately 6,000 amphibian species being globally threatened and at least 43% experiencing some form of population decrease (Stuart et al. 2004). In addition to threats on species diversity, concerns over amphibian loss are related to their role in ecosystems' structure and function. Although the latter is poorly studied still (Wells 2007), amphibians comprise the highest fraction of vertebrate biomass in many ecosystems (Blaustein et al. 1994, Gibbons et al. 2006), being essential food supply for predators (Blaustein and Wake 1995), significant consumers of algae and phytoplankton (Whiles et al. 2006) and keystone predators of invertebrates (Davic and Welsh 2004, DuRant and Hopkins 2008). Due to their trophic importance, environmental sensitivity, research tractability, and impeding extinction, amphibians have been adopted as model taxa in ecological research for studying the impacts of habitat loss, pollution, disease, and global climate change (Hopkins 2007).

Amphibians' susceptibility to environmental perturbations is related to their biological, ecological and behavioural features, such as heavily permeable skin, complex life cycle, use of multiple habitats, dependence on water, and limited dispersal ability (Wells 2007). Despite (or even thanks to) such apparent limitations of amphibians, the group as a whole has been remarkably successful in evolutionary terms – amphibians have persisted over hundreds of millions of years regardless of the dramatic global changes in climate and habitat structure (Delfino 2005, Blaustein and Bancroft 2007). However, the speed of environmental changes today apparently exceeds the rate at which amphibians can adapt (Wells 2007). The resulting population declines are known or suspected to be caused by various anthropogenic factors, often acting in concert: habitat loss and degradation, spread of pathogens and alien species, global warming, enhanced ultraviolet radiation, increased environmental acidity, contaminants, and over-exploitation (Alford and Richards 1999, Semlitsch 2000, Blaustein and Kiesecker 2002, Collins and Stofter 2003, Beebee and Griffiths 2005, Cushman 2006, Gardner et al. 2007).

Of these modern threats to amphibians, habitat loss and degradation are the most obvious factors and acute stressors globally (Alford and Richards 1999, Blaustein and Kiesecker 2002, Gardner et al. 2007) and the main drivers of amphibian declines in Europe (Joly et al. 2003, Stuart et al. 2004). Because Europe has a long history of anthropogenic conversion of land cover, amphibians went into a severe decline there much earlier than elsewhere (Houlahan et al. 2000, Buckley and Beebee 2004). At the same time, however, this has given them the longest time to adapt to anthropogenic secondary habitats. Therefore, European studies on long-term effects of habitat loss and the history of amphibian population declines – which in many European regions are poorly documented still (Houlahan et al. 2000) – might be relevant also for other continents.

Two main aspects of the impact of habitat degradation on amphibians should be highlighted. First, to complete their complex life cycles, most amphibians require multiple habitats, including distinct breeding, foraging and hibernation or aestivation sites, as well as a permeable migration matrix to connect and buffer these elements (Gibbs 1993, 2000, Semlitsch and Bodie 2003). Most commonly amphibians breed in freshwater habitats and spend the rest of the activity period in the surrounding terrestrial habitats or they move between different habitats for reproduction, foraging and hibernation (Skelly et al. 1999, Marsh and Trenham 2001, Semlitsch 2008, Stevens and Baguette 2008). Thus, amphibians may be threatened by the degradation of just one part of their habitat or of the matrix, even if the other parts remain intact. That makes them particularly vulnerable to a range of anthropogenic processes such as conversion of natural landscapes to agricultural and urban ecosystems, road building, intensification of agriculture and timber harvesting (Semlitsch 2000, Alford et al. 2001, Cushman 2006, Baldwin and deMaynadier 2009). In Europe, a great variety of such impacts have been documented (Table 1), but large changes have taken place in other parts of the world as well. For example, the replacement of native forests with monoculture plantations has reduced amphibian species diversity in North America (deMaynadier and Hunter 1995) and southeastern Australia (Parris and Lindenmayer 2004), the clearing of forest for arable land has caused the loss of amphibian species in Madagascar (Andreone et al. 2005), and clear-cutting for timber has reduced salamanders' species richness and harmed their local populations (with an estimated loss of 75–80% of individuals) in North Carolina (Petranka et al. 1993).

Second, habitat loss and degradation also reduce the connectivity of habitat patches (Fahrig 2003, Fischer and Lindenmayer 2007), which may decrease population size, wane immigration from other populations, thus impeding demographic rescue effects, decrease genetic variability and diminish population fitness (Joly et al. 2003). Poor connectivity affects amphibians due to their generally low dispersal rates (Bowne and Bowers 2004), although that impact may differ among species according to their different mobility (e. g. Green 2003, Schabetsberger et al. 2004, Funk et al. 2005, Semlitsch 2008) and the ability to cross unsuitable areas between habitat patches. For example, in landscapes highly altered by agriculture and urban development in northern Italy, populations of the Italian crested newt (*Triturus carnifex*) and the common toad (*Bufo bufo*) became isolated, while the Italian tree frog (*Hyla intermedia*) and the edible frog (*Rana* kl. *esculenta*) easily crossed the landscape matrix using the network of ditches and hedgerows (Ficetola and Bernardi 2004). The natterjack toad (*Bufo calamita*), another ground-dwelling species, does not cross extensive areas of unsuitable terrain between habitat patches (Beebee and Denton 1996) and the movement ability of its juveniles is strongly affected by land cover type (Stevens et al. 2004). Similarly, migration efficiency of juvenile American toads (*B. americanus*) and spotted salamanders (*Ambystoma maculatum*) is related to land cover type and distance between the aquatic and terrestrial habitat (Rothermel 2004). Reductions in genetic diversity, caused by the lack of connectivity between populations, have been demonstrated in urban populations of the common frog (*Rana temporaria*) in England (Hitchings and Beebee 1997) and in the toad *Rhinella ornata* in Brazilian coastal forests (Dixo et al. 2009). Thus, low recruitment of dispersing individuals (both juveniles and adults), caused by poor connectivity of the habitat matrix, can play a major role in the decline and extinction of amphibian populations (Sinsch 1992, Sjögren–Gulve 1998).

Despite the fact that habitat loss and degradation are obvious factors of population dynamics in general, and amphibian declines in particular, their impacts on amphibians are known in surprisingly general terms only (Alford and Richards 1999, Blaustein and Kiesecker 2002, Beebee and Griffiths 2005, Cushman 2006). The necessity for a considerably increased research effort (Hazell 2003, Gardner et al. 2007) requires paying more attention to threatened species, their habitat conservation practices, and population and metapopulation issues in specific landscape contexts (Brito 2008). Also, basic knowledge on species-specific habitat requirements is still needed to reliably predict population responses to changes in habitat area or isolation (Cushman 2006) and, thereby, to protect, restore or create habitat patches of high quality (Marsh and Trenham 2001) and to connect them to functional networks (Stevens and Baguette 2008).

Within that agenda, there are four general gaps of knowledge regarding the loss and degradation of amphibian habitats, which are addressed in this thesis. First, there is a need for organizing, for management purposes, the great variability among and within amphibian species in terms of their habitat requirements and sensitivity to landscape change. Although species-specific management approaches are preferred (Cushman 2006, see also **IV**), that knowledge is often lacking and in some cases even the species level is too general – different populations of the same species may react differently to the same stressor or their combination (Blaustein and Kiesecker 2002). An outstanding but poorly studied case of the latter are the *high-latitude and high-altitude populations*, which, due to environmental stress, may be unable to recover quickly from disturbance, and are thus particularly vulnerable to extinction (Morrison and Hero 2003, Beebee and Griffiths 2005).

Table 1. Examples of documented habitat-loss related declines in the European amphibian populations

Species	**Area**	**Observed time period and extent of decline**	**Cause**	**Source**
Salamandra salamandra	Littfeld, Germany	1965–1985. Population went extinct.	Replacement of deciduous forest with coniferous plantations.	Schmidt et al. 2005
Euproctus platycephalus	Sardinia	Early 1980s–2001. The extent of decline was not estimated.	Alteration of aquatic habitat, pollution and waste disposal, introduction of alien fish, construction of dam and removal of water.	Lecis and Norris 2003
Triturus cristatus *T. helveticus, T. vulgaris*	Sussex, UK	1977–1996. Disappeared from 67%, 50% and 29% of breeding ponds respectively.	Destruction of aquatic habitats, succession after abandonment, fish introduction.	Beebee 1997
Triturus marmoratus, Pelobates cultripes, Bufo calamita	León, NW-Spain	1980s–1996. Not detected in 1996 any more in the area.	Degradation of aquatic habitat due to the introduction of red crayfish (*Procambatus clarkii*).	Rodriguez et al. 2005
Pelobates fuscus	Sweden	1959–1996. Disappeared from 86% of breeding ponds.	Loss of aquatic and terrestrial habitat due to urbanisation, artificial drainage and the intensification of road traffic.	Nyström et al. 2007
P. fuscus	Denmark	1945–1990. Disappeared from 96% of breeding ponds.	Loss of habitat due to intensification of agriculture, eutrophication, infilling, release of fish.	Fog 1988
Bufo calamita	UK	20th century until the 1970s. Disappeared from >75% of its historical sites.	Habitat destruction by agricultural reclamation, afforestation with conifer plantations, urban constructions, cessation of grazing, overgrowth, acidification.	Beebee et al. 1990, Denton et al. 1997
B. calamita	Ireland	19th century until the 1970s.	Habitat destruction due to drainage and agricultural improvements.	Beebee 2002
Hyla arborea	Lolland, Denmark	1981–1991. Disappeared from 68% of breeding ponds.	Loss of aquatic and terrestrial habitat due to draining, infilling of ponds, fish introduction, road building, intensification of agriculture.	Fog 1997, Andersen et al. 2004
Rana temporaria	Widi, Switzerland	1989–1997. Estimated population decline ca. 20% per year.	Degradation of aquatic habitat due to introduction of goldfish (*Carassius auratus*).	Meyer et al. 1998

At the interspecific level, the common knowledge in conservation biology that habitat loss most severely affects species having narrow habitat tolerance (Blaustein and Kiesecker 2002) should be explicitly addressed, because it is not obvious which species are actually in question and how that should translate into management actions. In addition to the technical problems with measuring niche breadth (Lawton 1993, Fridley et al. 2007), the basic relationship between ecological niche and rarity of species is still debated in ecological theory. That relationship should be explicitly explored in terms of two habitat-related hypotheses: *the niche breadth hypothesis* (Brown 1984) and *the niche position hypothesis* (Gaston 1994). The niche breadth hypothesis claims that the species attaining large geographical distributions and occurring at high local densities are capable of this because they occupy a broader range of habitats and exploit diverse environmental conditions and resources (Brown 1984). In accordance with the niche position hypothesis, abundant species use resources, which are common in the particular area and time, while rare species utilize locally scarce and restricted resources (Gaston 1994, Gaston et al. 1997). The niche breadth hypothesis highlights the specialization process; notably that species tend to specialize simultaneously in different dimensions of their multidimensional niche. In contrast, the niche position hypothesis includes the idea of niche conservatism (e.g. Wiens and Graham 2005), which means that species carry their historically evolved habitat requirements in a dynamic world – so that their distribution follows habitat availability in a particular time period. In terms of conservation, the niche breadth hypothesis implies great difficulties with maintaining or creating conditions for viable populations of rare (highly specialized) species in the human-dominated world – unless these species adapt to new conditions. According to the niche position hypothesis, habitat restoration seems a more promising approach because habitat-limited species may only require some, not many, specific conditions to be restored.

Second, *numerical responses* of amphibian populations to habitat change are poorly described, especially the process of extinction along with habitat loss and fragmentation (Andrén 1994). For establishing such relationships, large spatial scales should be involved (Ovaskainen and Hanski 2003) and *long-term data* are required to separate the deterministic response of population to habitat loss from annual fluctuations (Pechmann et al. 1991, Gardner 2001, Marsh 2001). The majority of studies identifying critical habitat loss thresholds of population responses have focused on birds and small mammals (e.g. Andrén 1994, 1997, Carlson 2000). The few such studies on amphibians have explored the threshold effects in relation to the watershed disturbance (Willson and Dorcas 2003) or forest cover (Gibbs 1998, Homan et al. 2004, Denoël and Ficetola 2007), demonstrating that the critical thresholds vary by spatial scale and species, and are also sensitive to the statistical methods used (Homan et al. 2004, Denoël and Ficetola 2007). Sometimes populations do not respond immediately to habitat change, but exhibit time lags (Brooks et al. 1999). Concerning amphibians, the time lag effects have been observed in relation to the habitat destruction and species diversity (Findlay and Houlahan 1997, Löfvenhaft et al 2004).

Third, the view on amphibian habitats has often been too narrow. Most studies have focused on relationships between forest cover and species occurrence (Gardner et al. 2007). However, the generalised suggestion that high forest cover benefits amphibians may not apply to species that are fully aquatic or depend on nonforested habitats (Cushman 2006). Thus it is also essential to establish habitat requirements of species in terms of the extent and pattern of *nonforest habitats*. Additionally, the use of multiple habitats by amphibians (see above) and the metapopulation dynamics of several aquatic-breeding species (Marsh and Trenham 2001) require landscape-level studies to explore the effects on habitat destruction (Storfer 2003, Cushman 2006). That knowledge is also essential for informing conservation managers as to how to renew the ecological integrity of degraded habitat matrices and create self-sustaining systems for long-term persistence of resident populations (Petranka and Holbrook 2006), including their metapopulation structure (Semlitsch 2002).

Fourth, the research on amphibian habitat loss and degradation should, at best, be closely linked to *practical conservation management* both by improving the current practices and using the information gained by management efforts (Gascon et al. 2007). That gap of knowledge is highlighted by the scarcity of successful examples of habitat restoration for threatened amphibians worldwide (Denton et al. 1997, Briggs 1997, 2001, Petranka et al. 2007), even when the restoration has been specifically targeted to such species (Nyström et al. 2007, Briggs et al. 2008).

This thesis consists of four case studies, which explore the impacts of habitat loss and restoration on declining amphibian populations in the European temperate zone. Study **I** presents a quantitative example of population-level effects of habitat loss at a large spatial scale and over a long time period, thus addressing the second and third gap of knowledge described above. For the first time the land cover changes in Baltic coastal meadows were measured and numerically related to their specific amphibian species, the natterjack toad. That analysis of the process and consequences of habitat loss is based on a 30-year data set, which allowed (1) reconstructing the historical distribution of the toad populations and analysing it retrospectively in relation to quantitative changes in habitats; (2) determining whether particular habitat components were critical for the survival of the species. Study **II** uses the same study species but focuses on the geographical context and a mechanism behind breeding-habitat requirements. In this way, it targets the first and fourth gap of knowledge highlighted above. This study is novel in demonstrating a complex relationship among environmental stress, breeding habitat selection, and faster growth and development of the tadpoles of the natterjack toad at the northern edge of its range. The constraints found highlight the necessity for geographically explicit approaches in habitat conservation.

The general patterns of habitat requirements are further explored in study **III**, comparing two coexisting newt species, which are having contrasting population trends: the smooth newt (*Triturus vulgaris*) and the crested newt (*T. cristatus*). Those closely related species provided a unique opportunity to explore the habitat-related explanations to the rarity of species (see above) and, thereby, the habitat restoration potential for amphibians. Finally, in study **IV**, that knowledge on habitat requirements was put into practice and the effects were monitored (cf. the fourth knowledge gap). Study **IV** describes a large-scale restoration project targeted at two threatened pond-breeding amphibian species: the crested newt and the common spadefoot toad (*Pelobates fuscus*). It demonstrates, in accordance with the predictions from study **III**, that habitat restoration for threatened species can rapidly increase their numbers if the restoration is implemented at the landscape scale, taking into account the habitat requirements of target species and the ecological connectivity of populations. Additionally, this management study also provides a useful protocol for the creation of breeding habitats for threatened amphibians.

2. METHODS

2.1. Study species

The studies focused mainly on two threatened amphibian species: an anuran – the natterjack toad (**I, II**), and an urodele – the crested newt (**III, IV**). According to the IUCN criteria these species are of 'least concern' (IUCN 2009); however, their populations have overall decreasing trend and are threatened in the northern part of their distribution range. The species are also listed in the annexes of the EU Habitats Directive (92/43/EEC), thus requiring specific conservation efforts to achieve favourable conservation status.

The natterjack toad is a European endemic species, distributed from the Iberian Peninsula in the southwest to the Baltic coast in the east; and reaching the northern edge of its range in Estonia (Sinsch 1998). Throughout its distribution area this toad inhabits early successional habitats that are inherently unstable: generally open (nonforested) areas with bare ground and low vegetation, and shallow sun exposed (usually ephemeral) ponds with warm water and few predators (Denton et al. 1997). Due to such distinctness of its habitats, and considering the substantial decline of the natterjack toad in its natural sites over the northern part of the distribution range (Sinsch 1998, Buckley and Beebee 2004), this toad is an ideal object to explore the impacts of habitat changes in different landscapes (**I**). Additionally, as the natterjack toad occurs in similar habitats (coastal meadows and sand dunes as the primary sites, and sand and gravel pits as secondary sites) around the Baltic Sea, one can study the behavioural differences of this species in similar habitats at high and low latitudes (**II**).

The crested newt is a mainly aquatic amphibian species that occurs in northern and central Europe (Arnold 2002). Despite of its fairly large distribution area, the crested newt has declined in most of its range countries (Edgar and Bird 2006), most obviously because of habitat degradation (Beebee 1997, Joly et al. 2001, Stumpel 2004, Skei et al. 2006). Interestingly, although this species can often be found in the same landscapes and water bodies with the closely related smooth newt (Zuiderwijk 1986, Griffiths and Mylotte 1987, Skei et al. 2006, van Buskirk 2007), the same environmental processes have not affected the latter to such an extent. Therefore that species-pair, consisting of a rare and a common species, was used as a model for exploring habitat-related hypotheses of the rarity of species in study **III**. In the habitat restoration study (**IV**), pond colonisation by the crested newt and another threatened species – the common spadefoot toad – was described and habitat characteristics essential for that were analysed. The common spadefoot toad has decreased dramatically within its northern distribution range (Fog 1988, Nyström et al. 2002, 2007), including the range edge in Estonia. So far only limited conservation work has taken place for the crested newt (Edgar and Bird 2006). Aquatic habitat restoration targeted to the common spadefoot toad has preserved some declining populations in Denmark (Fog 1997); nevertheless, the reproductive success (Nyström et al. 2007) and colonisation rates of the species (Fog 1997, Stumpel 2004, Briggs et al. 2008) have remained low. Therefore the design of a successful large-scale habitat restoration project for those species might serve as an important example of habitat restoration for threatened amphibian species in general.

2.2. Study areas

The fieldwork was carried out in Estonia and Denmark: the studies **I** and **IV** in Estonia, study **III** in Denmark, and study **II** in both countries. The study area **I** represented most of the known historical distribution range of the natterjack toad in Estonia, including the four counties of western Estonia: the two large islands Saaremaa and Hiiumaa, and Pärnu and Lääne counties on the mainland (Figure 1A). For study **II** seven local populations of the natterjack toad were sampled from the study area **I**, and six populations were selected from Denmark. Two Estonian and four Danish populations inhabited coastal meadows and the rest were in sand or gravel pits, reflecting the current situation of the natterjack toad's habitats in Estonia and Denmark. Those study sites (**II**) were distributed over the latitudinal gradient from 54ºN to 59ºN. In order to compare the characteristics of the toad's breeding ponds in the two countries, the depth and the surface area of all ponds were measured in each site and the ponds with spawn strings (up to four per site; a total of 10 ponds from each country) were sampled in April 2007. In addition, the breeding site selection of the natterjack toads (study **II**) was explored using the data on colonisation of 20 new ponds in Estonia. Those ponds were created in 2000–2002 in two coastal meadows and in 2000–2006 in five sandpits, in order to improve the breeding conditions of the existing natterjack toad populations there.

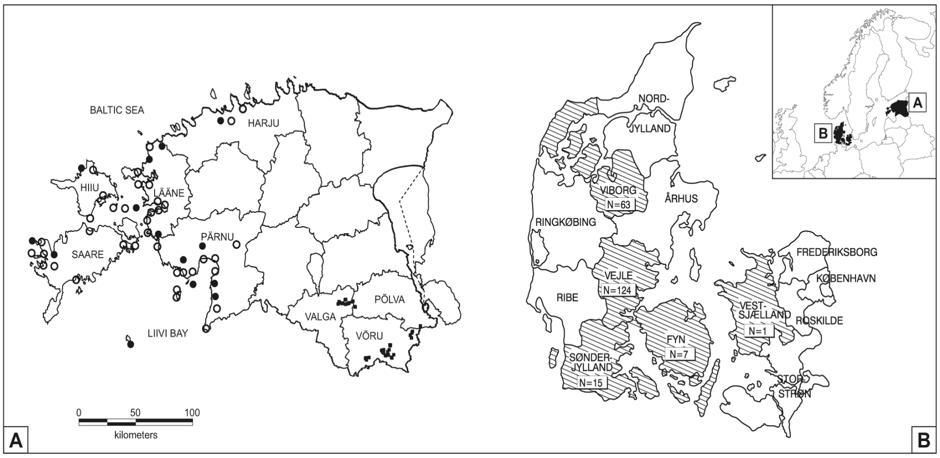

Figure 1. The study areas. (A) Estonia. Distribution of the natterjack toad is indicated with hollow circles (historical sites where the species was present in the 1930s; N = 52) and filled circles (extant sites where the species was present in 2005; N = 14)(**I**). Small squares are the constructed ponds (N = 230) in southern Estonia (**IV**). (B) The study counties in Denmark (striped) with the numbers of investigated ponds (**III**).

To determine the habitat requirements of the crested newt and to compare those with the habitat demands of the smooth newt (study **III**), 210 ponds were inventoried in central and southern Denmark where both species co-occur (Figure 1B). The ponds were situated in the four main landscape types of Denmark: forest, semi-natural habitats, mosaic landscapes with extensive agriculture, and intensively managed agricultural land. One hundred ponds had been restored or dug a new by the conservation authorities between 1992 and 2002; the rest being natural depressions or water bodies created by local people (for cattle or hunting; marl or peat).

That descriptive research was followed by a practical habitat restoration study in Estonia (**IV**), which involved two largest LPAs (the Haanja LPA and the Otepää LPA) of the southern part of the country and four smaller protected areas (Sadrametsa, Piusa, Hauka, Karste) in the same region (Figure 1A). As land cover type appeared essential for the crested newt (**III**), the areas of habitat restoration were carefully selected. The hilly moraine landscape of the Haanja LPA represents a mosaic of forests (45%), grasslands (21%) and small extensively used fields and farmlands. The Otepää LPA (42% forest) also has a varied hilly relief, but the fields are generally larger than in Haanja though intensive farming practices are not in use. Altogether, 405 natural and man-made ponds were inventoried before the restoration in Haanja and Otepää, and 230 ponds in 27 clusters (4–26 ponds in each; the distance between ponds less than 500 m) were finally restored or created in the study area.

2.3. Field methods

Detecting amphibians. The main research unit for all four studies was a 'site', which was defined considering particular species and its habitat. In studies **I** and **II** the 'site' was defined as an area of suitable terrestrial and aquatic habitat supporting a natterjack toad population (Buckley and Beebee 2004), i.e. the 'site' was roughly equalized with a local population. In studies **III** and **IV** the 'site' denoted a pond and its surrounding area up to 50 m – a typical migration distance of adult crested newts (Jehle 2000).

To detect amphibians – the natterjack toads (**I**, **II**), the smooth newts and the crested newts (**III**), and all local amphibian species (**IV**) – several field methods were used in the sites: searching for individuals along night transects and for calling males in the breeding ponds (**I**), searching for spawn strings, eggs or egg-clutches (**I**, **II**, **IV**), and dip netting of larvae (**I**–**IV**). In study **II**, the caught tadpoles were photographed, in order to measure their length (see below) and to detect the developmental stage.

Due to a single visit to each pond in studies **III** and **IV**, random effects in the number of caught individuals were probably large, thus only presence-absence of species was used for analyses. Although the 'absences' may include some undetected 'presences', their frequency was probably small (see **III**). On the other hand, by focusing on finding eggs and larvae (i.e. detecting breeding attempts) the ‘presences’ probably do not contain many marginal habitats, which might confound the niche determination (**III**; Pulliam 2000, Hirtzel and Le Lay 2008) or essential habitat characteristics for pond colonisation (**IV**).

In case of the Estonian natterjack toads (study **I**), several visits were made during the spring and summer 2000, 2002 and 2004 to determine its current presence in the sites where the species occurred in the 1930s. When toads were not found in a historical location, searches were extended to all suitable habitat patches within 1 km. Additionally, new sites supporting natterjack toad populations were searched since 1997 all over Estonia. To detect the species, all the field methods listed above were used. In addition to the fieldwork, historical data on the distribution and habitats of the species in Estonia were collected from published sources, monitoring programs (since 1985) and field records of the Estonian herpetologists (since 1997). These data were used to reconstruct the toad’s population history and to estimate its long-term population losses. According to the data character, three periods where identified when the natterjack toad was thoroughly studied throughout Estonia and the records were accurate enough to depict locations on maps: the 1930s, the 1970s–1980s, and 1997–2005.

To explore the habitat requirements of the crested newt and the smooth newt in Denmark (**III**) and to study the colonisation of constructed ponds by amphibians in southern Estonia (**IV**), the fieldwork was carried out by several herpetologists in the summers 2004–2005 (**III**) and 2005–2008 (**IV**). Due to the numerous observers, data collection was carefully standardized and simplified. The main method was standard dip-netting of larvae (Skei et al. 2006). In each pond, dip-netting included ten sweeps covering important microhabitats for newts (**III**) or was performed during 10 minutes (**IV**). The invertebrate ‘by-catch’ of the dip-netting was used to characterize the diversity of food base of the newts (e.g. Griffiths and Mylotte 1987; **III**), while eggs of newts and egg-clusters of the “green frogs” (the pool frog *Rana lessonae* and the edible frog) were additionally searched for in study **IV**. For each pond, the presence of fish was estimated using the combined data of visual observation, dip-netting and information from local people (**III**, **IV**). Breeding attempts of amphibians in the constructed ponds were ascertained by the presence of eggs and/or larvae (**IV**).

Measuring the growth rate of the natterjack toad’s tadpoles (**II**)**.** In 2007, all the study sites (populations) were repeatedly visited (2–4 times) in April to detect the onset of natterjack toads’ reproduction. To follow the growth and development of tadpoles, four visits were made to each site synchronously in Estonia and Denmark (1–2 May, 15–16 May, 1–2 June and 15–16 June) covering all the main phases of larval development from hatching to metamorphosis. During every visit, 20 tadpoles from each pond were caught. The tadpoles were photographed in a plastic box equipped with dimensional grids and filled with 5 mm of pool water, and released to their natal pond thereafter. The developmental stage of the spawn and larvae was determined according to the Gosner’s (1960) gradation. From the photographs, the snout-vent body length of the tadpoles was measured.

Assessing habitat characteristics. In order to determine the habitat demands of the crested newt and the smooth newt (**III**), 18 aquatic and 11 terrestrial features were assessed for each studied pond in Denmark. The set of the habitat variables was based on their potential importance to larval and adult newts. Land cover type was studied within 50-m radius from each pond (see Jehle 2000). To characterize potential immigration sources in the framework of metapopulation structure, distance to the nearest pond occupied by conspecifics as well as the numbers of other ponds nearby, were estimated for four distance classes up to 800 m (the maximum migration distance of juvenile crested newts; Kupfer and Kneitz 2000).

In southern Estonia the pre-restoration pond quality for amphibian breeding was estimated in June 2005 (**IV**). A pond was considered of high-quality for amphibians' reproduction if no extensive negative effects were observed, such as complete overgrowing, eutrophication, silting (a thick mud layer) or shade (more than 80% of the water table). In order to detect habitat characteristics essential for successful colonisation of ponds by the target species (the crested newt and the common spadefoot toad), seven aquatic and one terrestrial habitat feature were described in the field for each restored or created pond in the third year after the pond construction started (in June 2008). Similarly to study **III**, the land cover type within 50 m of a pond and the distance to the nearest pond occupied by conspecifics were assessed.

2.4. GIS analyses

For study **I**, all the Estonian natterjack toad's sites since the 1930s were first recorded in a GIS, using a digital base map of Estonia. Then, to explore changes in the coastal grasslands in relation to their toad populations, land cover was described in 32 of the 46 coastal meadow sites where the natterjack toad had been recorded in the 1930s. The land cover composition was measured from aerial photographs (scale 1:10 000) taken in 1950–1951, 1970–1971 and 1996–2000. As earlier aerial photographs were unavailable, those from 1950–1951 were used to interpret the population data of the 1930s because land use in the early 1950s was still similar to that in the 1930s (Ratt 1985, Luhamaa et al. 2001). The toad sites were delineated at two spatial scales – 2-km and 6-km coastal stretches (running 1 and 3 km in either direction from the recording locality, respectively) – based on the natterjack toad's maximum dispersal ability (Sinsch 1997, 1998). The width of the stretch was on average 200–300 m. Based on published data on the toad's habitat demands (Beebee 1979, 2002, Boomsma and Arntzen 1985), four habitat components were distinguished for the analysis: (1) small water bodies and shallow depressions; (2) managed (grazed, mowed) coastal meadows; (3) open sandy areas; and (4) reed beds (*Phragmites australis*) that had developed during the natural succession of unmanaged grasslands and comprised a 'lost habitat' for the natterjack toad. Together, the first three components comprised the 'habitat complex' for the species. The borders of the habitat components were digitalized from the three sets of aerial photos and their areas were measured within each stretch using MapInfo software.

2.5. Data processing

Most analyses were performed with the Statistica 7.0 (Statsoft, Inc.) software package. For hypothesis testing mostly multivariate methods (GLM, multivariate logistic regression, ANOVA) and conventional parametric tests (t-test; Pearson's correlation) or – if the assumptions of the parametric tests were not met – non-parametric tests (U-test, Kruskal-Wallis ANOVA, Spearman correlation, χ^2-test, Wilcoxon matched-pairs test) were used. To discriminate between occupied-unoccupied sites (**III**, **IV**) or survived-extinct populations (**I**), multiple logistic regression models were built, according to the procedure of Hosmer and Lemeshow (1989).

To compare niche breadths of pond-breeding species (**III**), we used the generalist-specialist metric (θ) derived from the beta diversity of amphibian communities (Fridley et al. 2007). The use of θ is based on the assumption that specialist species, on average, should co-occur with fewer species than generalists. In 100 simulations for each species, we randomly selected 20 ponds of its occurrence and calculated beta diversity of the sub-sample by subtracting from the total amphibian species richness the average number of species per pond.

Geographical differences in the length of the natterjack toad's tadpoles were analysed using a mixed ANOVA (SAS procedure MIXED; **II**). Analogously, generalised linear models with random effects (SAS procedure GLIMMIX) were applied to analyse the differences in the developmental stage between countries and dates.

3. RESULTS

3.1. The natterjack toad and the Baltic coastal meadows

According to the historical data, the natterjack toad mainly inhabited managed coastal grasslands (89% of all known sites; Figure 2) in the 1930s in western Estonia (**I**). However, since the 1980s those grasslands have lost their value as the main habitat for the toad, while the importance of secondary habitats has increased. By the 2000s, only 8% of the historical sites were still occupied. Although 82% of the 17 extant populations now inhabit secondary habitats (Figure 2), the occupation of the new habitats has not balanced the loss of historical sites in primary (coastal grassland) habitats.

The decrease of the natterjack toad in West-Estonia was less dramatic before 1970 (43% sites lost) than after this date (81% of the remaining 16 sites; $\chi^2_{1,\,adj} = 4.7$, $p = 0.031$) (**I**). When the time period was taken into account, the only habitat variable that remained significant for distinguishing between occupied and extinction sites was the area of managed meadows and open sandy areas at the beginning of the period. Larger areas of these land-cover types were related to better survival of toad populations. In the landscapes historically occupied by natterjack toads, the area of managed coastal meadows declined while reed beds expanded in each of the four counties studied and in both of the post-1950 periods (Table 2). In addition, open sandy areas were substantially reduced or lost entirely.

By 2000, as compared to 1950, areas of the entire habitat complex for toads had declined by 83% in Saare County, 82% in Lääne County, 65% in Pärnu County, and 60% in Hiiu County (**I**). Over the same period, the natterjack toad became extinct in all historical sites in Lääne County, in 90% of sites in Pärnu County, in 88% of sites in Saare County, and in 75% of sites in Hiiu County. Hence, extinction rates exceeded relative rates of habitat loss in each county. Again, this pattern was most evident after 1970 (in the advanced stages of habitat loss), when rates of population loss exceeded habitat loss by 32 ± 7% (SE), a significant deviation from zero ($t_3 = 4.4$, $p = 0.022$). Prior to 1970, there was no such deviation in rates (1 ± 1%). In both periods of study, natterjack toad population decline was greatest in the counties with the worst habitat loss (Figure 3).

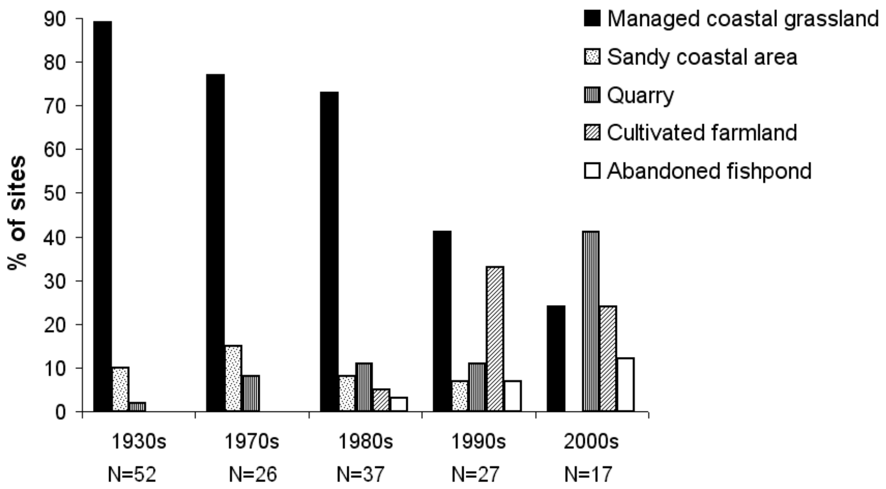

Figure 2. Habitat classifications of Estonian natterjack toad sites over five decades (**I**).

Table 2. Total area of habitat components at historical natterjack toad sites in four counties in western Estonia (**I**).

Land cover type and period	***Area (ha)***				
	Hiiu (4 sites)	Saare (8 sites)	Lääne (9 sites)	Pärnu (11 sites)	Total (32 sites)
Managed coastal meadow					
1950–1951	1101	1332	2157	819	5409
1970–1971	1069	496	1049	428	3042
1996–2000	873	253	789	354	2269
Wet depressions and ponds					
1950–1951	791	279	2341	422	3833
1970–1971	177	335	1629	230	2371
1996–2000	20	86	17	94	217
Open sandy areas					
1950–1951	332	756	18	128	1234
1970–1971	22	51	0	103	176
1996–2000	0	64	0	27	91
Reed beds					
1950–1951	76	128	1639	26	1869
1970–1971	185	339	3030	231	3785
1996–2000	461	612	3145	748	4966

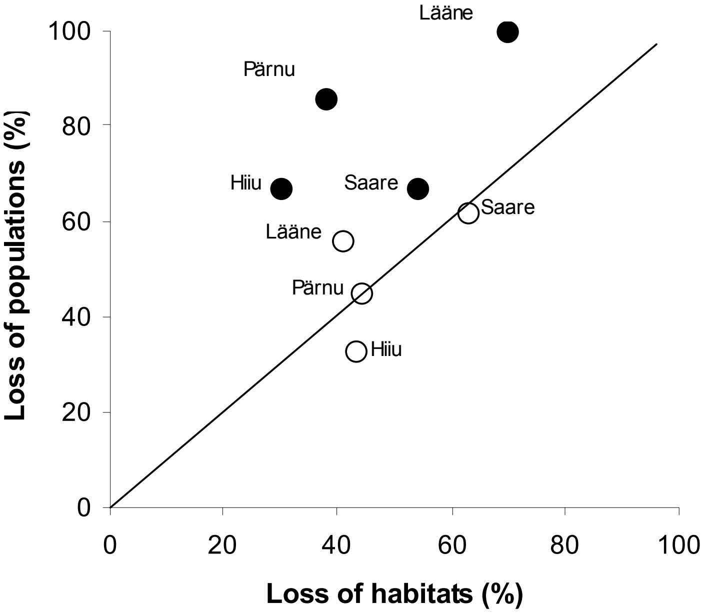

Figure 3. Natterjack toad population loss in relation to the loss of its coastal meadow habitats between the 1930s–1960s (hollow symbols) and the 1970s–2000 (filled symbols) in four Estonian counties. The diagonal line denotes a 1:1 relationship. (**I**)

In Estonia, where the breeding season of the natterjack toad started, on average, 12 days later than in Denmark, the species clearly preferred shallower ponds, while the Danish toads preferred deeper ponds (Figure 4). Importantly, the mean water-depth of the ponds in the study sites did not differ between the countries (ANOVA: $F_{1,\ 49} = 0.1$, $p = 0.70$) (**II**). In Estonia, the artificial-pond colonisation for breeding depended both on the depth (logistic regression: coefficient = –0.47, SE = 0.29, log-likelihood = –13.4, $\chi^2_1 = 19.0$, $p < 0.0001$) and the area of the pond (coefficient = 139.1, SE = 94.7, log-likelihood = –7.3, $\chi^2_1 = 6.9$, $p = 0.009$). All the colonised water bodies but one had a maximum water depth less than 40 cm (Figure 5).

On 1–2 May 2007, when only spawn strings or newly hatched tadpoles (Gosner stages 10–19) were found in the Estonian ponds, the tadpoles were swimming freely (stages 21–25) in the Danish ponds (**II**). However, by 1 June, the Estonian tadpoles had caught up the size and developmental stage of the Danish ones: 72% of the tadpoles in Estonia and 73% in Denmark had reached the stages 30–40, and no between-country differences could be detected for the developmental stage ($F_{1,\ 13.2} = 1.6$, $p = 0.22$) or for the length (0.85 vs. 0.87 cm, $F_{1,\ 14.8} = 0.4$, $p = 0.53$; Figure 6). Accordingly, when the data of these two sampling periods were combined, the highly significant country × date interaction both for the developmental stage ($F_{1,607} = 942$, $p < 0.0001$) and length ($F_{1,617} = 132$, $p < 0.0001$) indicated indisputably larger between-country differences on the earlier date. By the last sampling (15–16 June), most of the tadpoles had passed metamorphosis and had left the water bodies in both countries.

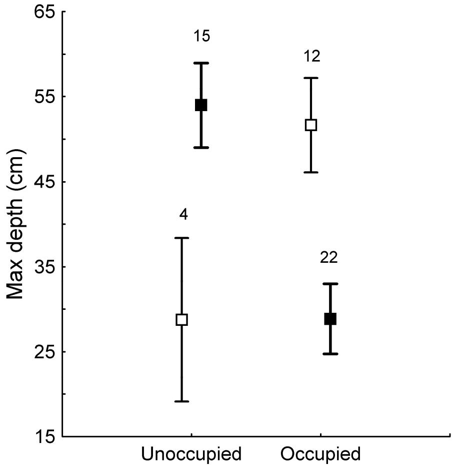

Figure 4. Maximum depth of water in April in the Estonian (filled symbols) and Danish (hollow symbols) natterjack toad sites according to whether they were occupied or not by the toads. The numbers refer to sample sizes; whiskers are 95% confidence intervals for the mean (**II**).

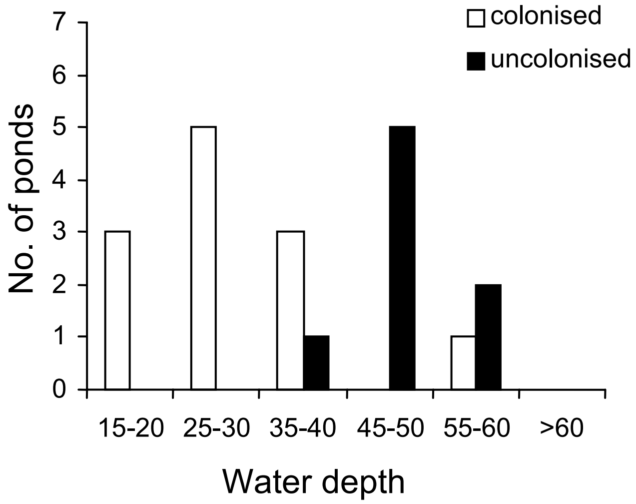

Figure 5. Maximum depth of water in the constructed ponds colonised and not colonised by the natterjack toads in Estonia (**II**).

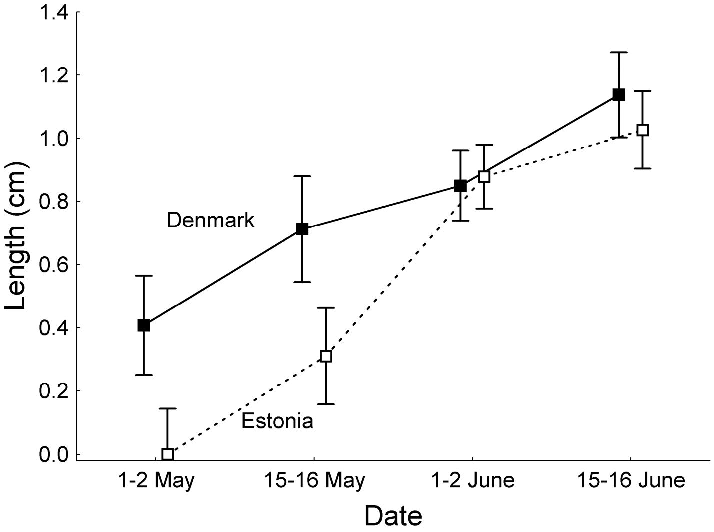

Figure 6. The mean length of the natterjack toads' tadpoles/metamorphosed toadlets (N = 20 per pond), measured in the Estonian and Danish study sites 2007. The whiskers are 95% confidence intervals (**II**).

3.2. The crested newt and pond management

The crested newt and the smooth newt coexisted in 59% of all ponds occupied by those species in Denmark (**III**). Although the smooth newt was more common and abundant (mean 11.2 ± 1.2 SE of caught individuals per occupied pond) than the crested newt (7.3 ± 0.7 SE), their niche breadth differences were not supported: beta diversity of the amphibian communities did not differ between the ponds occupied by the species. The simulation-based θ-values per 20 ponds were 4.2 ± 0.9 SE for the crested newt and 4.4 ± 0.8 SE for the smooth newt (**III**).

In Denmark the crested newt presence in a pond was explained by three characteristics (Table 3): land cover within 50 m, the number of invertebrate taxa in the pond, and the distance to the nearest pond occupied by conspecifics. Mixtures of open land and forest were always superior over a single land-cover type around the pond, and open lands were used in the sequence of their naturalness (dry grassland > meadow > field) (**III**). Land cover within 50 m turned out to be important (log-likelihood = –138.0, $\chi^2_6 = 18.1$, $p = 0.006$) also for the colonisation of constructed ponds by the crested newt in Estonia (**IV**). In Estonia the most favourable land cover type around the pond was forest, which, in combination with meadows and extensive farms, increased the pond suitability for the species. Smooth newt presence in the Danish study ponds was also explained by three characteristics (Table 3; **III**): the number of invertebrate taxa in the pond, sediment type (sand preferred; mud avoided), and the distance to the nearest pond occupied by conspecifics. In contrast to the crested newt, land cover type within 50 m did not approach significance even at the univariate stage of the analysis.

The pre-restoration inventory in the two protected areas in southern Estonia found only 22% of 405 ponds being of high-quality for amphibian breeding (**IV**). Forty-eight percent of the examined ponds were stocked with fish (mainly alien species), 15% were completely overgrown with dense vegetation and/or bushes, 10% were eutrophicated or silted up, and 5% were in shade. Among the seven amphibian species (including indeterminate green frogs) found in the area, the crested newt was still relatively common while the common spadefoot toad was the rarest species (Table 4). Similarly to the Danish study (**III**), the crested newt (as well as the smooth newt) avoided ponds with fish in southern Estonia. Moreover, the common spadefoot toad was never found in such ponds there (**IV**).

Table 3. Results of logistic regression models of habitat factors explaining the presence of the crested newt (*Triturus cristatus*) and the smooth newt (*Triturus vulgaris*) in 140 ponds in Denmark (**III**).

Variable	***Estimate***	***SE***	***LL***	χ^2	***p***
Triturus cristatus (model log-likelihood –72.7, p<0.0001)					
Land cover within 50 m (8 types)			–90.3	35.3	<0.001
Nearest *T.cristatus* pond	–0.21	0.14	–75.5	5.6	0.018
Invertebrate diversity	0.11	0.05	–75.5	5.6	0.018
Triturus vulgaris (model log-likelihood –68.5, p <0.0001)					
Sediment (4 types)			–66.3	16.4	<0.001
Nearest *T.vulgaris* pond	–0.82	0.37	–80.5	4.2	0.040
Invertebrate diversity	0.14	0.05	–74.5	12.0	<0.001

LL – log-likelihood of the variable.

In only three years (by 2008) when 22 of the 405 existing ponds were restored and 208 new ponds created in southern Estonia, the number of occupied ponds increased 6.5 times in case of the common spadefoot toad and 2.3 times in case of the crested newt (**IV**). The success was particularly clear at the pond-cluster scale: by 2008, the breeding attempts of the crested newt had been recorded in 92% of the pond clusters and breeding of the common spadefoot toad in 81% of clusters. In 2008, the 230 constructed ponds hosted, on average, 3.1 ± 0.1 SE amphibian species per pond, while the 405 non-restored ponds had 1.8 ± 0.07 SE amphibian species (t-test: $t = 11.2$, $p < 0.001$; **IV**).

The constructed ponds situated close to a source pond (i.e. inhabited by the species prior to restoration) were colonised more quickly than more isolated ponds both in the case of the crested newt: (Kruskal-Wallis ANOVA: $\chi^2_3 = 17.6$; $p < 0.001$) and the common spadefoot toad ($\chi^2_3 = 10.6$; $p = 0.014$). In terms of pond characteristics, the crested newt presence in constructed ponds was explained by the land cover type within 50 m (see above) and a higher cover of submerged vegetation in the pond (log-likelihood = –131.4, $\chi^2_1 = 4.8$, p = 0.028). The colonisation by the common spadefoot toad was explained by the transparency and colour of water (log-likelihood = –77.9, $\chi^2_3 = 8.3$, p = 0.04): transparent or clear but brownish water was favoured (97% of such ponds being colonised) and unclear, muddy or algae-green water was avoided (**IV**).

Also in Denmark the crested newt (as well as the smooth newt) occurred significantly more often in restored or created than in unmanaged ponds (**III**). The pond management success for the crested newt was highly dependent on the surrounding land cover: 89% of the 19 managed ponds in the preferred dry grasslands or dry grassland-forest mosaics were occupied, compared with 56% of the 70 ponds in other habitats ($\chi^2_1 = 8.5$, p = 0.004). However, management status contributed significantly to the multivariate model in the smooth newt only (log-likelihood = –73.1, $\chi^2_1 = 6.0$, p = 0.014); there was no such independent effect for the crested newt (log-likelihood = –72.6, $\chi^2_1 = 0.6$, p = 0.45; **III**).

Table 4. The occurrence of amphibian species in the 405 existing ponds in Haanja LPA and Otepää LPA in June 2005; in the constructed ponds over three years after restoration; and the total number of constructed ponds occupied by amphibians in 2008 (N = 230).

Species	***Ponds occupied in 2005***		***Post-restoration colonisation of constructed ponds (%)***			***Constructed ponds occupied in 2008***	
	N	%	I year N=230	II year N=193	III year N=111	N	Breeding attempt %
Triturus vulgaris	149	36.8	35.7	65.8	82.0	156	68.7
T .cristatus	94	24.2	16.1	54.9	71.2	127	98.4
Pelobates fuscus	8	2.0	5.2	15.0	15.3	29	96.6
Bufo bufo	86	21.2	23.9	30.1	41.4	76	65.8
Rana temporaria	90	22.2	25.7	37.3	44.1	95	86.3
R.. arvalis	62	15.3	17.8	22.8	40.5	85	87.1
“Green frogs”	236	58.3	19.1	55.4	82.0	144	54.2

4. DISCUSSION

4.1. Habitat loss impacts: the natterjack toad in coastal meadows

The main importance of case study **I** lies in documenting the long-term habitat loss in relation to population decline of a threatened habitat-restricted species in quantitative terms. In the first half of the 20th century, the model species – the natterjack toad – was widespread and abundant in managed (grazed or mowed) coastal grasslands along the coast of the Baltic Sea in Estonia, Sweden and Denmark (Kauri 1947, Fog 1988, Andren and Nilson 2000, Briggs 2004). Later, intensive large-scale agriculture, drainage (Beintema 1991) and lack of management (Koivula and Rönkä 1998, Ottvall and Smith 2006) have degraded these meadows to the extent that they are among the most threatened habitats in Europe (Annex I of the EU Habitats Directive, 92/43/EEC), and the natterjack toad has declined or disappeared in most of its coastal meadow sites (Fog 1988, Andren and Nilson 2000, Briggs 2004). That species has suffered also in other parts of its range due to habitat degradation: in Britain (Denton et al. 1997), Ireland (Beebee 2002) and Germany (Bast 1994, Sinsch 1998).

Since the 1930s, coastal meadow habitat complexes declined 60–83% in the natterjack toad's sites in western Estonia, while the toad populations declined 91% (**I**). Such a substantial loss of coastal meadows can be attributed to social and economic factors. Between 1945 and 1991, and especially in the 1960–80s, drainage and excessive use of fertilizers negatively affected hydrology and water quality, and altered natural succession and heterogeneity of the meadows (Ratt 1985). Due to eutrophication, reed expanded rapidly after the 1960s (Soikkeli and Salo 1979). In addition, coastal pastures and hayfields of low productivity were gradually eliminated (Ratt 1985).

Such habitat degradation can be expected to affect natterjack toads in multiple ways, but three characteristic and possibly general aspects for amphibians should be highlighted as documented by study **I**. First, as expected from the complicated structure of amphibian habitats (see Introduction), habitat degradation was not a simple, uniform process, but distinct by habitat components, and those components differentially affected the population viability. The significance of particular habitat components in the decline of the natterjack toad has been documented elsewhere as well. In England the primary reason was the loss of breeding grounds (Beebee and Denton 1996), while in south-west Scotland the population decreased due to loss of breeding ponds and coastal sandy grasslands (Fleming et al. 1996). In Estonia, sparsely vegetated or bare sandy areas, which provide foraging habitat and daytime shelter for the toads, declined the most: after grazing stopped, these areas became overgrown with reed (wet sites) or brushwood (higher sites). Similarly, shallow depressions and small water bodies overgrew with tall vegetation (reed, *Carex* sp., *Scirpus* sp., *Salix* sp.) and decreased extensively in all four study counties. At the same time, large areas of managed coastal grassland and open sand significantly enhanced the survival of local toad populations. Because those relationships appeared for the areas at the beginning of the periods explored, they were most likely related to the key role of initial population size (large populations are more resistant to annual fluctuations, i.e. stochastic extinction; Halley et al. 1996, Marsh 2001).

Second, extinction rates of the toad populations were higher than total habitat loss rates throughout the study area, and this pattern appeared in the advanced stage of habitat loss (after the 1970s; **I**). This provided empirical support to the theoretical models, which have revealed nonlinear relationships between the area of original habitat, patch size and isolation of patches, on the one hand (Andrén 1994), and extinction probabilities on the other hand (Fahrig 2001). The previous studies have demonstrated that for forest dependent amphibians, such significant thresholds appeared at 20–40% of remaining forest cover (Gibbs 1998, Homan et al. 2004, Denoël and Ficetola 2007), while for stream salamanders, the threshold effect was found already when disturbed habitat reached to 20% of watershed (Willson and Dorcas 2003). Such a substantial difference between the extinction thresholds of species reveals to the necessity for further studies, particularly concerning threatened species.

There are three complementary explanations to the increased extinction rates of natterjack toad populations at the advanced stage of habitat degradation. (1) Some habitat components disappeared altogether, notably the temporary ponds on wet meadows due to excessive overgrowing and drainage effects. (2) Habitat fragmentation effects (Fahrig 2003) inducing population isolation (Funk et al. 2005). By that time, about half of the overall habitat complex had disappeared (Figure 3) and, as demonstrated by theoretical models, the isolation of habitat patches generally appears when roughly 40% or less of the original habitat has remained in the landscape (Andrén 1994). Moreover, the species having low dispersal rates and large area (or complex habitat) requirements are particularly sensitive to habitat fragmentation, especially if the habitat is dissected by hostile environments (Andrén 1996). Therefore, the effect of isolation not only depends on the distance between habitat patches, but also on the suitability of the surrounding matrix. This is also the case with the natterjack toad, which is known not to cross extensive areas of unsuitable terrain (Beebee and Denton 1996), for instance the dense reed beds in overgrown coastal meadows. (3) The changed habitat conditions (tall, dense vegetation) favoured competitors and predators, such as common toads (Banks and Beebee 1987 a, Bardsley and Beebee 2000) and grass snakes (Denton and Beebee 1996).

Third, although the natterjack toad is a pioneer species (Boomsma and Arntzen 1985) and also inhabits anthropogenic secondary habitats, the gradual colonisation of such habitats did not balance the loss of the primary (coastal grassland) habitat in Estonia, where 67% of populations were lost between the 1930s and 2000s (**I**). The possible reasons for that may include the smaller overall area or lower quality of those secondary habitats (sand and gravel pits) and, more generally, the rapid rate of the primary habitat loss compared with the colonisation of, and adaptation to, the novel habitats. Additionally, sand and gravel pits are often surrounded by hostile terrain (e.g. forest and plantations in Estonia), which does not allow the dispersal of individuals. Similarly, the poison dart frogs (*Dendrobates granuliferus*, *D. auratus*) occurred at remarkably low densities in secondary sites compared to the pristine forest habitats in southwestern Costa Rica, which referred to the low quality of the secondary habitats (Miller and McFarlanei 2007). Although some tropical secondary sites (monocultures) can bear viable amphibian populations if the area is large and special management practices have been taken into consideration, the long-term effect of such sites on amphibians is not known (Becker et al. 2007). Moreover, in many types of secondary habitats, natural succession proceeds rapidly once human activities cease. For example, in a stone quarry in Germany the natterjack toad population declined 37% in five years due to natural succession of the breeding ponds (Münch and Schröer 1994). In such places, species dependent on habitats of early successional stages cannot persist without habitat-management efforts (Stevens and Baguette 2008, Warren and Büttner 2008). As shown in Germany, secondary sites alone cannot ensure the long-term survival of natterjack toad populations (Stephan et al. 2001).

4.2. Geographically varying habitat demands: the natterjack toad in Estonia and Denmark

Study **II** demonstrated that shallow breeding ponds (water depth no more than 40 cm), which were essential for the natterjack toad in Estonia, were not selected and used for breeding in Denmark. Hence, the habitat components critical for the toad at the northern limit of its range did not have a similar importance in another area. The study also described the apparent reason for such contrasting habitat selection: the necessity for rapid growth and development of tadpoles during a shorter activity period and in colder climate at the higher latitude. Despite a 12-day average difference in the onset of breeding of the species in Denmark and Estonia, the tadpoles passed metamorphosis at the same time in both countries (**II**). Although synchronised metamorphoses, despite asynchronous spawning, have been previously recorded in British natterjack toad populations, the causal mechanisms have remained unexplored (Beebee 1985 a).

Shallow water has been regarded to support tadpole growth because it warms up rapidly and is more oxygenated (Blaustein and Bancroft 2007). Hence, adaptation to such habitats might explain the paradoxically higher temperature optima reported for northern amphibians (Ståhlberg et al. 2001). On the other hand, because shallow ponds were not used for breeding by the natterjack toads in Denmark, such ponds expectably possess risks (such as desiccation; e.g. Newman 1992) that are outweighed only at higher latitudes. In Estonia, the ponds selected for breeding were not only shallow, but also extensive, which may reduce the risks of intraspecific competition of tadpoles (Tejedo and Reques 1994) and desiccation. A similar preference by the species for large breeding ponds has been demonstrated in northern England (Banks and Beebee 1987 b). Additionally, in shallow water the tadpoles may be more vulnerable to avian (Sherman and Morton 1993) or mammalian predators (Day and Linn 1972) and more exposed to damaging UVB radiation (Blaustein and Bancroft 2007) – those risks might be mitigated by shorter metamorphosis time and fewer invertebrate predators in shallow ponds at high latitudes.

The importance of shallow ponds for amphibian development at high latitudes reveals a direct, physiologically set link between habitat selection and geographic range. First, while ‘habitat availability’ is known to limit species’ ranges (Holt et al. 2005), study **II** illustrated that ‘habitat’ may differ across the range because of physiological constraints. Therefore, delineating potential ranges according to the availability of ‘typical’ habitats is risky unless the mechanisms determining habitat quality are explicitly known. Specifically, the importance of ephemeral water-bodies (e.g. Griffiths 1997, Adams 1999) and impacts of their loss on amphibians may be particularly pronounced at the climatically determined range edges, where the species have to cope with environmental stress. Second, even the mechanistic models used to predict range changes in response to climate change (Peck et al. 2009) do not incorporate behavioural plasticity (notably habitat selection), which appeared a major factor facilitating successful breeding of natterjack toads in Estonia. Therefore, the geographically varying habitat requirements of a species should be determined and their relation to the species’ life history traits explored, especially in case of threatened species, in order to realize species distribution limits, and protect and restore its habitats (see also Constible et al. 2009). Without such knowledge the species conservation attempts may fail, because habitat determinants vital in certain areas (e.g. range margins) have not been met. However, those relations have remained largely unexplored. In this sense study **II** is one of the rare examples demonstrating that the geographically varying breeding habitat selection ensured the faster growth and development of the high-latitude amphibian tadpoles, which implies that genetic effects (previously demonstrated in common garden studies; e.g. Laugen et al. 2003, Lindgren and Laurila 2005) and environmental effects combine to produce the latitudinal gradients of phenotypic variation.

4.3. Habitat availability as a cause for rarity: the crested newt and the smooth newt in Denmark

Study **III** indicated that the large geographical distribution and higher local densities of the smooth newt compared with those of the crested newt (e.g. Griffiths and Mylotte 1987, Stumpel 2004) are unlikely to be explained by a different level of habitat specialisation of these species. The narrower habitat tolerance hypothesis was rejected both in the analysis of habitat requirements and community variability – beta diversity of the amphibian communities did not differ among the ponds occupied by the newt species. Instead, the crested newt's rarity and/or declining trend could be related to its niche position in relation to the currently prevailing conditions as indicated by qualitative differences in the key demands of the newts. Therefore, rarity in this species pair was not a consequence of narrower adaptations or specialisation to environmental conditions and resources, as hypothesized to be a general rule by Brown (1984), but rather a consequence of the availability of essential environmental conditions and resources (e.g. habitat) at a given time (Gaston 1994, Gregory and Gaston 2000). Consequently, it seems that the species carry their historically evolved habitat requirements in a dynamic world – so their distribution follows changes in habitat availability.

The major difference in the habitat characteristics of the crested newt and the smooth newt in Denmark was the importance of the terrestrial land cover around the pond: while the most natural habitats (particularly a mixture of dry grassland and forest) were essential for the crested newt, the surrounding habitat lacked any effects on the smooth newt (**III**). That result was also confirmed in Estonia: crested newts more frequently colonized the ponds constructed in the vicinity of forest or in landscapes with mosaics of forest and grassland than those in open landscapes (**IV**). Therefore the rarity or declining trend of the crested newt may have been caused by the replacement of natural forest and grassland mosaic with arable lands, and the further intensification of agriculture. These changes are particularly pronounced in Western Europe, which is indeed the area of the greatest reductions in the newt populations (**III**).

Differing abilities of the crested newt and the smooth newt to use terrestrial habitats have been described by Müllner (2001) who found that most of the crested newts leaving the pond, oriented towards the forest, while smooth newts often stayed under grass tufts and dead wood in the wet zone of the pond and 25% of the individuals migrated to open grasslands. The importance of forest for the crested newt has been repeatedly noticed all over its range (Jehle and Arntzen 2000, Joly et al. 2001, Skei et al. 2006). Forest provides abundant food, shelter and hibernation sites, and increases the connectivity of the landscape, enhancing dispersal possibilities (Laan and Verboom 1990, Joly and Miaud 1993, Schabetsberger et al. 2004, Skei et al. 2006). However, in particular settings (e. g. range margins), forest and scrub may be vital also for the smooth newt, as demonstrated in Britain (Beebee 1977, Beebee 1985 b), in Ireland (Marnell 1998) and in Norway (Skei et al. 2006). Such difference in the smooth newt's landscape cover preferences may refer to its geographically varying habitat selection, as demonstrated in the case of the natterjack toad in study **II**. However, concerning the smooth newt, further research would be needed confirming this possible explanation.

For the smooth newt, the type of pond sediment appeared important in Denmark, but that effect cannot be excluded for the crested newt either because occupancy rates varied in a similar way in both species (sand > clay > mud > peat). Therefore, this habitat characteristic has probably lower explanatory power to elucidate the contrasting conservation status of those two newt species (**III**).

A diverse invertebrate community in a pond was preferred by both newt species. This characteristic indicates a direct measure of food supply for the newts. Given that feeding niche partitioning may be even more important than microhabitat partitioning for the coexistence of these generalist predators (Griffiths and Mylotte 1987, van Buskirk 2007), its inclusion as a part of the habitat models (see Hall et al. 1997) clearly improved their relevance for determining the key habitat characteristics for the newts.

4.4. Habitat restoration for threatened amphibians

Studies **I–III** and the practical restoration project described in study **IV** provided several essential requirements of habitat restoration for threatened amphibians. In fact, some of these findings (**I–III**), in combination with previous knowledge and management principles (e.g. Semlitsch 2002), were already successfully implemented in aquatic habitat restoration for the crested newt and the common spadefoot toad in Estonia (**IV**).

First, as demonstrated in the natterjack toad (**I**)**,** population extinction rates may exceed habitat loss rates, particularly in the advanced stage of habitat loss. Therefore, habitat degradation should be stopped and restoration initiated before habitat loss becomes too extreme. Otherwise, the populations might decline or become restricted to isolated habitat fragments to such an extent that natural colonisation of restored habitats is not possible. Although in such cases translocation may be an option, it poses additional concerns with the eventual spread of diseases (Hamer and McDonell 2008) or mixing up the species' genetic material stemmed from different populations (Trenham and Marsh 2002). The translocation process is also time-consuming (Griffiths and Pavajeau 2008) and costly (Seigel and Dodd 2002). A good example for this principle was the rapid colonisation of the constructed ponds by the crested newt and the common spadefoot toad in southern Estonia, where habitat restoration began when remnant populations of those species were still strong (**IV**).

Second, habitat restoration should be targeted at critical (limiting) habitat qualities for threatened species, because those species are not necessarily narrow specialists in every respect (**III**). For the crested newt, the areas with a mixture of forest and natural or semi-natural open habitats (e.g. dry grasslands) should be given a priority (**III**, **IV**) and, if necessary, restoration of such terrestrial habitats should be considered in degraded landscapes (Briggs 1997, Denton et al. 1997). For the natterjack toad (and possibly for most species), restoration of large areas should be prioritised because such areas enhance the survival of local populations for several reasons (**I**): they contain all essential habitat components, can host larger populations and may thereby be essential for maintaining metapopulation dynamics (e. g. Semlitsch 2002).

Third, even vital habitat requirements of a species may differ across its range, they should be determined and considered for habitat restoration. For instance, water depth (maximum 40 cm) should be taken into account when restoring breeding habitats for the natterjack toad at high latitudes, while ponds of similar depths may be avoided by the species at lower latitudes (**II**).

Fourth, while the general necessity for a landscape-scale approach in habitat restoration for amphibians is well known (e.g. Semlitsch 2002), the Estonian restoration project highlighted the success of a specific technique – water bodies for pond-breeding species should be restored or created in clusters. When appropriately planned – considering distances between the ponds in relation to the dispersal abilities of target species (Jehle 2000, Nyström et al. 2002, Semlitsch 2008) and the preferences of breeding adults to return to natal ponds (Jehle and Arntzen 2000) – the clustered configuration increases colonisation probabilities of the ponds and secures the ecological connectedness of the metapopulations (Semlitsch 2002, Petranka et al. 2007). Hence, creating ponds in clusters helps to ensure the long-term persistence of populations (Halley et al. 1996). As demonstrated in study **IV,** the crested newt and the common spadefoot toad indeed colonised significantly more rapidly the constructed ponds situated closer to source ponds (already inhabited by the species) than the ponds further away. Therefore, to increase colonisation possibilities and secure small populations dependent on a single breeding pond, some ponds should be created or restored in the close vicinity of existing source ponds. For such planning, local distribution of target species should be determined before the restoration starts (**IV**).

Additionally to the species-specific habitat requirements, described above, some general guidelines should also be followed when constructing ponds for amphibians, especially for threatened species. For example: (i) ponds should have shallow littoral zones of submerged vegetation and rapidly warming water to provide suitable egg-laying, foraging and refugium sites for amphibians and their larvae (Semlitsch 2002, Porej and Hetherington 2005). For the crested newt, the availability of submerged vegetation apparently increased pond colonisation (**IV**). As an exception, the breeding ponds of early-successional species, such as the natterjack toad, should be poorly vegetated (Beebee and Denton 1996) or submerged vegetation should be kept low (e.g. by grazing) (**I**); (ii) mineral sediments (clay and sand) in ponds should be favoured, as they usually provide clear and transparent water of relatively higher pH and oxygen level. Such sediments were similarly favoured by the smooth newt, the crested newt and the common spadefoot toad (**III**, **IV**). In ponds with peat or mud, humic substances lead to lower pH and often also low oxygen concentrations (Brönmark and Hansson 2005). (iii) the constructed ponds should be separated from running water to avoid fish introduction, sedimentation or pollution. Fish are a major limiting factor for pond-breeding amphibians (e.g. Joly et al. 2001, Brönmark and Hansson 2005, Denoël et al. 2005, Skei et al. 2006, Nyström et al. 2007; **III**, **IV**). Also, creating ponds in clusters (see above) allows constructing water bodies with different hydroperiods, using in this way natural pond-drying to prevent and eliminate predation (Semlitsch 2002).

Finally, in order to construct a high-quality aquatic habitat for amphibians (especially for threatened species), the participation of experienced amphibian experts in the field is essential (**IV**). As each pond construction is unique (depending on relief, soil, hydrology, presence of drainage systems, surrounding habitats etc.), it may be difficult for unexperienced persons to make right decisions according to the habitat requirements of certain amphibian species.

5. CONCLUSIONS

This thesis explored the essential habitat determinants, impacts of habitat loss and habitat restoration possibilities for threatened amphibian species in Estonia and Denmark. A long-term study on the natterjack toad populations in Estonian coastal meadows revealed that (i) at the landscape-scale the extinction rates of local populations exceeded habitat loss, and this pattern appeared at the advanced stage of habitat loss; (ii) large areas of managed meadow and sand were essential for the survival of natterjack toad populations. However, the following between-country comparison demonstrated that the habitat qualities critical for the growth and development of natterjack toad tadpoles varied geographically – the ponds selected for breeding at high latitudes were significantly shallower than the ponds at low latitudes. Consequently, the key habitat requirements of a species may vary geographically, thus these should first be determined and thereafter considered in habitat conservation and restoration. The comparison of the habitat requirements of two coexisting newt species with contrasting population trends demonstrated similar breadths of their ecological niches but different key demands: the quality of terrestrial habitats (mixture of forest and open grassland) was essential for the crested newt but not for the smooth newt. Instead of a narrower habitat demand, the crested newt's rarity and declining trend could be related to its niche position in relation to the currently prevailing conditions. By supporting the niche-position hypothesis of rarity, this study indicated that habitat restoration should be targeted at critical (limiting) habitat qualities for threatened species as those species are not necessarily narrow specialists in every respect. A practical aquatic-habitat restoration for the crested newt and the common spadefoot toad in southern Estonia demonstrated that habitat restoration for threatened pond-breeding amphibians can be successful indeed if it is biologically based, implemented at the landscape scale, taking into account the habitat requirements of target species and the ecological connectivity of populations. That project is one of the few successful habitat restoration examples for threatened amphibians in Europe.

SUMMARY IN ESTONIAN

Elupaikade hävimise ja taastamise mõju kahepaiksetele

Liikide väljasuremine inimtegevuse tagajärjel on viimastel aastakümnetel pannud looduskaitsebioloogе selle protsessi põhjusi otsima ja võimalikke lahendusi leidma. Kõrgemate taksonoomiliste rühmade hulgas on kahepaiksed ühed kõige ohustatumad: ligi 43% teadaolevatest liikidest on langeva arvukusega. Kahepaiksed on ümbritseva keskkonna suhtes tundlikud nii bioloogiliste (õhuke tundlik nahk, moondega areng), ökoloogiliste (sõltuvus ühtaegu nii maismaa- kui vee-elupaikadest) kui ka käitumuslike (vähene liikuvus) omaduste tõttu. Kuna kahepaiksed vajavad eluks nii toitumis-, varjumis- ja talvitumispaiku maismaal kui ka sigimispaiku vees ning liiguvad aktiivsusperioodi jooksul nende vahel, siis ohustab neid ainuüksi ühe elupaigakomponendi hävimine või komponentide vahelise ühenduse katkemine. Piiratud liikumisvõime tõttu on kahepaiksed väga tundlikud ka elupaikade killustumise suhtes. Seetõttu peetakse elupaikade hävimist kahepaiksete kadumise üheks peamiseks põhjuseks. Ometi on elupaikade hävimise mõju kahepaiksete asurkondadele vähe uuritud, seda eriti ohustatud ja haruldaste liikide, nende elupaikade kaitse ning populatsioonide ruumilise struktuuri ja dünaamika seisukohast.

Doktoritöö on seotud nelja olulise teadmistelüngaga elupaikade hävimise mõju kohta kahepaiksetele. Esiteks: kuna kahepaiksete elupaigaomadused erinevad liigiti, siis tuleks neid looduskaitses käsitleda liigipõhiselt, see aga ei ole praktikas alati võimalik. Samuti võivad sama liigi elupaigaomadused levila piires oluliselt erineda, näiteks tasandikel ja mägedes või erinevatel laiuskraadidel, mida seni on aga vähe uuritud. Oluline on leida ka üldisi seaduspärasid, mida saaks laiendada väheuuritud liikidele ja situatsioonidesse. Eeskätt on arvatud, et elupaikade hävimine mõjutab just kitsalt kohastunud liike, aga liigid, keda peetakse teatud elupaigatingimustele kitsalt spetsialiseerunuks, võivad olla ka generalistid, kellele sobiv elupaik on antud ajal ja kohas lihtsalt haruldane. See erinevus on oluline elupaikade taastamise seisukohast. Teiseks on ebapiisavalt teada, kuidas elupaikade hävimise mõju asurkondadele arvuliselt prognoosida. Kolmandaks: enamik uuringuid elupaikade hävimise mõjust kahepaiksetele on tehtud metsa-ökosüsteemides, mille tulemused pole aga üldistatavad liikidele, kes asustavad avamaastikke või märgalasid. Neljandaks ei leia elupaiku käsitlevad uurimistulemused enamasti rakendamist ja kontrollimist liigikaitses elupaikade praktilisel säilitamisel ja taastamisel.

Töö hõlmab nelja uuringut, mis põhinevad Eestis ja Taanis läbi viidud välitöödel. Peamisteks uurimisobjektideks valiti kaks levila põhjaosas ohustatud kahepaikseliiki – kõre (*Bufo calamita*) ja harivesilik (*Triturus cristatus*). Kõre on selgelt eristuvate elupaigakomponentide tõttu sobiv mudelliik elupaigamuutuste ja nende mõjude uurimiseks asurkondadele. Lisaks võimaldas pikaajaline andmestik kõre esinemise kohta (alates 1930. aastatest) välja selgitada muutused liigi levikus ja elupaigakasutuses Eesti levila piires (Saaremaal, Hiiumaal, Läänemaal ja Pärnumaal). Ajalooliste aerofotode analüüsiga näidati arvuliselt kõre elupaikade vähenemise ulatust rannaniitudel ja seostati see liigi vähenemisega. Kuna kõre asub Eestis oma levila põhjapiiril, siis uuriti kõre elupaiganõudluse (kudemisveekogude suuruse ja sügavuse) ning kõrekulleste kasvu ja arengu geograafilisi erinevusi võrdlevalt seitsmes Eesti ja kuues Taani kõreasurkonnas. Harivesiliku kasutamine mudelliigina tulenes tema üldisest langevast populatsioonitrendist kogu levila ulatuses. Samas esineb harivesilik väga sageli koos lähiliigi – tähnikvesilikuga (*Triturus vulgaris*), kes on aga Euroopa üks tavalisemaid kahepaikseid. Selline liigipaar kahest koosesinevast, kuid erineva populatsioonitrendiga liigist võimaldas võrrelda liikide ökoloogiliste niššide laiust ja sisulisi erinevusi liigi harulduse võimalike seletustena. Selleks inventeeriti Taanis 210 väikeveekogu ja analüüsiti vesilike esinemist seal 29 elupaigatunnuse osas. Neid harivesiliku elupaiganõudluse andmeid rakendati omakorda Lõuna-Eestis 340 väikeveekogu taastamisel ja rajamisel. Eesmärgiks oli välja selgitada veekogude taastamise tulemuslikkus ohustatud liikidele ja selle mõju kogu piirkonna kahepaiksete faunale. Taastatud ja rajatud väikeveekogusid seirati kolmel järjestikusel aastal. Tehti kindlaks kahepaiksete esinemine veekogudes ning analüüsiti veekogude ja nende ümbrusega seotud tunnuseid, et välja selgitada, mis määrab veekogude asustamist harivesiliku ja samuti ohustatud liigi – mudakonna (*Pelobates fuscus*) poolt.

Kõre puhul leiti, et 1930. aastatel asus 89% Eesti asurkondadest majandatud rannaniitudel, aga 2000. aastateks moodustasid rannaniiduasurkonnad kõigist teadaolevatest asurkondadest vaid 8%. Samal ajal vähenes majandatud rannaniitude pindala kõre elupaikades eri maakondades 60–83% võrra. Kõre asurkondade väljasuremise ulatus ületas oluliselt elupaikade hävimise, seda eriti elupaikade hävimise viimases faasis, kui säilinud oli alla 40% elupaikadest. Selline seos väljasuremise ja elupaikade hävimise kinnitab teoreetilisi mudeleid väljasuremikünniste kohta, kusjuures ebaproportsionaalselt tugev mõju lõppfaasis võis olla põhjustatud nii 1) ajutiste madalaveeliste veekogude (peamiste kudemispaikade) täielikust hävimisest rannaniitudelt selleks ajaks, 2) elupaikade killustumisest kui ka 3) muudest muutunud elupaigatingimustest (nt. kõrge taimestik, mis on ebasobiv kõrele, soodustab konkurentide ja looduslike vaenlaste levikut). Kuigi kõre asustas samaaegselt ka teiseseid elupaiku (peamiselt liivakarjääre), ei kompenseerinud see rannaniitude kadumisega seotud populatsiooni vähenemist. Selle põhjuseks võib olla teiseste elupaikade väike pindala (Eestis on liivakarjäärid enamasti ümbritsetud metsaga) või nende madalam kvaliteet. Rannaniitudel osutus kõre jaoks määravaks suurte majandatud niidualade ja avatud liivaalade kadumine (kinnikasvamine). Suurte elupaigalaikude olulisus on ilmselt seotud populatsioonide algse suurusega. Suuremad asurkonnad on arvukuse kõikumiste ning seega ka väljasuremisohu suhtes vähem tundlikud kui väikesed ning killustatud asurkonnad. Lisaks asusid majandatud niidualadel kõre peamised kudemispaigad (suured ja madalaveelised lombid). See, et kõre koebki Eestis tunduvalt madalamatesse veekogudesse kui Taanis ja et sellel on sigimisbioloogiline seletus, selgus kõrekulleste arengu võrdlevas analüüsis. Hoolimata keskmiselt 12 päeva hilisemast kudemisajast jõudsid Eesti kõrekullesed arengus Taani liigikaaslastele järele ning moone toimus Taanis ja Eestis samaaegselt. Seega valivad kõred Eestis, levila põhjapiiril kudemisveekogusid, mis tagavad kulleste kiire arengu, nii et vaatamata lühemale vegetatsiooniperioodile saavad moonde läbinud kõred enne esimest talvitumist toituda ja areneda vähemalt sama kaua kui nende liigikaaslased madalamatel laiuskraadidel. Kokkuvõttes võib järeldada, et elupaigakomponendid, mis osutuvad liigi säilimise seisukohast olulisteks levila ühes osas (nt äärealadel), ei pruugi seda olla levila teistes piirkondades.

Harivesiliku ja tähnikvesiliku elupaigatingimuste võrdlev analüüs näitas, et hoolimata kahe liigi erinevatest populatsioonitrendidest ei erinenud nende liikide ökoloogilised nišid laiuse poolest. Mõlema liigi jaoks olid määravad kolm elupaigatunnust, millest kaks (toidubaasi mitmekesisus ja liigikaaslaste poolt asustatud veekogu lähedus) olid kummalgi liigil samad. Erinevuseks osutus maismaaelupaiga tähtsus harivesilikule, mis ei mõjutanud mingilgi määral tähnikvesiliku esinemist. Tõenäoliselt ongi harivesiliku langev populatsioonitrend seotud liigile olulise maismaaelupaiga (metsa ja loodusliku või pool-loodusliku rohumaa mosaiik) vähenemisega Lääne-Euroopas. Seega ei pruugi liigi haruldus olla tingitud liigi üldiselt kitsast kohastumisest, vaid hoopis mõne olulise elupaigatingimuse olemasolust antud ajaperioodil.

Kahepaiksetele olulise sigimispaiga – väikeveekogude – taastamisel ja rajamisel Lõuna-Eestis lähtuti eelnevalt tutvustatud uuringute tulemustest: (1) veekogude taastamist alustati enne, kui ohustatud liigid (harivesilik ja mudakonn) ja nende olulised elupaigad olid piirkonnas veel säilinud; (2) elupaikade taastamisel lähtuti liigiomastest elupaiganõuetest (nt rajati harivesiliku veekogud metsa lähedusse); (3) veekogude kiireks asustamiseks ja asurkondade pikaajaliseks säilimiseks rajati väikeveekogud kogumikena, arvestades seejuures kahepaiksete piiratud liikumisvõimet; (4) kogumikes loodi erineva sügavusega veekogusid, mis tagab (loodusliku ärakuivamise kaudu) kaladeta veekogude olemasolu igas kogumikus. Kolme aasta möödudes, kui veetaimestik oli jõudnud välja areneda, leidus harivesilikke 71% ning mudakonni 15% veekogudes. Samas oli mudakonna poolt asustatud veekogude hulk piirkonnas kasvanud 6,5 korda ja harivesiliku poolt asustatud veekogude hulk 2,3 korda. See projekt näitas, et kahepaiksete asurkondi on võimalik edukalt taastada, kui arvestatakse liikide elupaiganõudeid, nende meta-populatsiooni struktuuri ning taastatakse elupaiku suuremahuliselt, maastiku tasandil. Eestis läbiviidud väikeveekogude taastamine ja rajamine mudakonnale ja harivesilikule on üks vähestest edukatest ohustatud kahepaiksete elupaiga taastamise näidetest Euroopas.

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II. Research history

Scientific publications

Rannap, R., Lõhmus, A., Jakobson, K. 2007. Consequences of coastal meadow degradation: the case of the natterjack toad (*Bufo calamita*) in Estonia. – Wetlands 27, 390–398.

Rannap, R., Lõhmus, A., Briggs, L. 2009. Niche position, but not niche breadth, differs in two coexisting amphibians having contrasting trends in Europe. – Diversity and Distributions 15, 692–700.

Rannap, R., Lõhmus, A., Briggs, L. 2009. Restoring ponds for amphibians: A success story. – Hydrobiologia 634, 87–95.

Conference presentations

"Conservation of *Bufo calamita* in Estonia" (oral presentation), 8th Nordic Herpetological Symposium. Lund Sweden 24–26 July 2003.

"Restoration of ponds for threatened amphibians in Estonia" (oral presentation), International Pond Conference. Trieste, Italy 20–22 May 2005.

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"Decline of the natterjack toad (*Bufo calamita*) at the northern edge of its distribution range along with the degradation of coastal meadows" (oral presentation), 1st European Congress of Conservation Biology. Eger, Hungary, 22–26 August 2006.

"Pond requirements of coexisting newts: why is *Triturus cristatus* more vulnerable than *Triturus vulgaris*?" (oral presentation; co-authors: A. Lõhmus, L. Briggs), 16th European Congress of Herpetology. Porto, Portugal 19–24 September 2007.

"Niche position rather than niche width, differs in two coexisting amphibians having contrasting trends in Europe." (oral presentation; co-authors: A. Lõhmus, L. Briggs), 6th World Congress of Herpetology. Manaus, Brazil 17–22 August 2008.

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II. Teaduslik ja arendustegevus

Teaduslikud publikatsioonid

Rannap, R., Lõhmus, A., Jakobson, K. 2007. Consequences of coastal meadow degradation: the case of the natterjack toad (*Bufo calamita*) in Estonia. – Wetlands 27, 390–398.

Rannap, R., Lõhmus, A., Briggs, L. 2009. Niche position, but not niche breadth, differs in two coexisting amphibians having contrasting trends in Europe. – Diversity and Distributions 15, 692–700.

Rannap, R., Lõhmus, A., Briggs, L. 2009. Restoring ponds for amphibians: A success story. – Hydrobiologia 634, 87–95.

Ettekanded konverentsidel

“Conservation of *Bufo calamita* in Estonia” (suuline ettekanne), 8th Nordic Herpetological Symposium. Lund, Rootsi 24.–26. juuli 2003.

“Restoration of ponds for threatened amphibians in Estonia” (suuline ettekanne), International Pond Conference. Trieste, Itaalia 20.–22. mai 2005.

“Impact of habitat destruction to the natterjack toad *Bufo calamita* populations in Estonia, and the results of habitat restoration” (suuline ettekanne), 9th Nordic Herpetological Symposium. Värska, Eesti 15.–21. juuni 2006.

“Decline of the natterjack toad (*Bufo calamita*) at the northern edge of its distribution range along with the degradation of coastal meadows” (suuline ettekanne), 1st European Congress of Conservation Biology. Eger, Ungari, 22.–26. august 2006.

“Pond requirements of coexisting newts: why is *Triturus cristatus* more vulnerable than *Triturus vulgaris*?” (suuline ettekanne, kaasautorid: A. Lõhmus, L. Briggs), 16th European Congress of Herpetology. Porto, Portugal 19.–24. september 2007.

“Niche position rather than niche width, differs in two coexisting amphibians having contrasting trends in Europe.” (suuline ettekanne, kaasautorid: A. Lõhmus, L. Briggs), 6th World Congress of Herpetology. Manaus, Brasiilia 17.–22. august 2008.

“Successful large-scale habitat restoration for threatened amphibians in Estonia” (suuline ettekanne, kaasautorid: A. Lõhmus, L. Briggs), 2nd European Congress of Conservation Biology. Praha, Tšehhi Vabariik, 1.–5. september 2009.

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