

Breeding success of the threatened great crested newt in boreal forest ponds

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Amphibian declines have been reported worldwide during the last decades. In this study, we focused on the endangered great crested newt (*Triturus cristatus*), which has suffered from intensive forestry and past mire ditching in the northern verge of its distribution. We collected data from 46 breeding ponds in eastern Finland during 2005–2011 using dip-netting. We modeled breeding success with cost-effective methods by using site-level forest data. The results highlight the importance of herb-rich forests in the vicinity of breeding ponds. Based on the results possible new breeding sites can now be located based on the presence and size of types of nutrient-rich forest, proportion of deciduous trees, young stands, shading and unfavorable habitats in the vicinity of ponds. Also practical conservation measures, like creating new ponds within a certain area, can now be allocated more accurately using the same variables.

Introduction

Amphibian species constitute a threatened species group, which has severely declined worldwide (Stuart *et al.* 2004, Beebee & Griffiths 2005). In Europe, 59% of amphibians have decreasing populations, and nearly a quarter of amphibian species are considered threatened (Houlahan *et al.* 2000, Denoël & Ficetola 2008, Temple & Cox 2009). This decline of amphibians has a number of possible causes, ranging from habitat loss to chemical pollution, diseases and introduced species (Beebee & Griffiths 2005, Denoël & Lehmann 2006, Denoël & Fic-

etola 2008). In Europe, the main drivers of the decline have been habitat loss and degradation, as indicated by the fact that in Europe more than 60% of freshwater habitats have an unfavorable conservation status (European Commission 2009, Temple & Cox 2009). Moreover, habitat requirements of amphibian species are often quite demanding, because they also need suitable terrestrial habitat close to their aquatic breeding habitat.

Great crested newt (*Triturus cristatus*) is at present considered a threatened species, e.g. in Austria, Belgium, Czech Republic, Estonia, Finland, France, Latvia, Lithuania, Luxemburg,

Netherlands, Norway, Romania, Slovakia and Switzerland (Maurin 1994, Schmidt & Zumbach 2005, Edgar & Bird 2006, Gollmann 2007, Jacob & Denoël 2007, Tartes *et al.* 2008, Arntzen *et al.* 2009, Kålås *et al.* 2010, Terhivuo & Mannerkoski 2010, AmphibiaWeb 2012). Though the species is rare and has clearly declining populations in many parts of its distribution, it may still remain relatively common in suitable habitats (Arntzen *et al.* 2009, Denoël 2012). It has been included in Annexes II and IV of the European Habitats Directive and has received a Species Action Plan (Edgar & Bird 2006). This status calls for intensive research on environmental factors governing the distribution and abundance of newt populations, which is a prerequisite for effective conservation and management planning (Edgar & Bird 2006, Denoël & Ficetola 2008, Gustafson *et al.* 2011).

Although the great crested newt has been the subject of several studies (Edgar & Bird 2006, Karlsson *et al.* 2007, Denoël & Ficetola 2008, Gustafson *et al.* 2011), our knowledge of the species' habitat requirements is still incomplete. First, the majority of the studies have been conducted in central and western Europe, where the species occurs in a human-modified landscape that is affected, e.g., by agricultural intensification, expansion of infrastructure and fish stocking (e.g. Edgar & Bird 2006, Denoël & Ficetola 2008, Joly *et al.* 2001). In these studies, the characteristics of forest vegetation surrounding breeding ponds has rarely been investigated in detail. In northern Fennoscandia, the species occurs at its northern range margin and generally occupies a forest-dominated landscape, where the factors affecting the species distribution and abundance are likely to be different as compared with those in southern European populations (Gustafson *et al.* 2006, 2009, 2011, Skei *et al.* 2006). Second, several modeling studies on amphibians and their dependence on habitat factors have employed presence-absence data (e.g. Pellet *et al.* 2007, Denoël & Ficetola 2008, Gustafson *et al.* 2009, 2011, Hartel *et al.* 2010, Gómez-Rodríguez *et al.* 2012, but *see* Joly *et al.* 2001, Denoël & Lehmann 2006). Presence-absence data are useful to assess distribution patterns of species and changes in them. However, such data provide little understanding of the

spatial and temporal trends in local populations (Beebee & Griffiths 2005). Furthermore, presence-absence models do not distinguish poor habitats from higher quality sites with more abundant populations, which is important in conservation planning (Denoël & Lehmann 2006). Third, where abundance data of the amphibians have been employed in the analyses, often only adult individuals have been considered (e.g. Joly *et al.* 2001, Denoël & Lehmann 2006). Improved understanding of the sites with the highest reproductive potential can be better achieved using estimates of abundance of juveniles (Knutson *et al.* 2004). Such information provides more detailed estimations of the populations' long-term persistence dynamics and local population dynamics than number or density of adults alone.

The great crested newt is classified as an endangered species in Finland (Terhivuo & Mannerkoski 2010), and moreover, its preferred habitat — native-forest ponds — is a threatened nature type (Ilmonen *et al.* 2008). The available data suggest that the species inhabits natural ponds in boreal forests, and the proximity of deciduous forests has a positive effect on its occurrence (Gustafson *et al.* 2011), but the factors affecting breeding success in forest ponds are poorly known. It is also likely that only a portion of ponds with suitable breeding conditions have been found hitherto. Thus, there is an urgent need to develop rapid and cost-effective methods to assess where in boreal regions the most suitable sites for the species are located. Practical methods are needed, since intensive forest management practices, which create open areas and favor coniferous monocultures in the vicinity of ponds, diminish the quality of breeding ponds and their surroundings (Patrick *et al.* 2006, Gustafson *et al.* 2011).

In this study, we model the breeding success of the great crested newt by relating habitat quality data to the density of larval populations in boreal, previously unstudied ponds. The main questions addressed were: (i) How do the terrestrial habitats affect the breeding success of the great crested newt, and (ii) how accurately can breeding success be modeled using existing forest inventory data, to support the search of suitable breeding ponds elsewhere? Additionally we investigated (iii) how well can the breeding

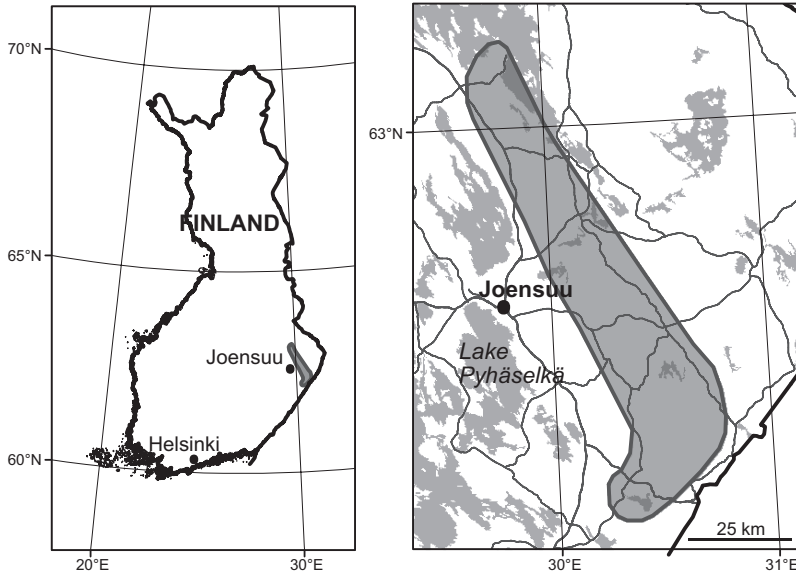


Fig. 1. The location of the study area in eastern Finland.

success of the great crested newt be explained using only the area and isolation of a given pond.

are subjected to intensive forest management for timber production. Clear-cutting is the principal harvest method.

Material and methods

Study site

In Finland, the great crested newt has a disrupted distribution separated by a 400-km-wide gap: (1) the region of Åland in the southwestern archipelago with circa 30 breeding ponds and (2) eastern Finland with 70 breeding ponds. This study covered the central parts of the Finnish distribution area located in the province of North Karelia in eastern Finland, extending from the municipality of Tohmajärvi ($62^{\circ}10'N$, $30^{\circ}19'E$) 120 km NNW to the Koli region ($63^{\circ}11'N$, $29^{\circ}49'E$) and forming a 20-km-wide belt (Fig. 1) at 80–347 m above sea level. Eastern Finland is sparsely populated, dominated by wide-ranging boreal coniferous forests (i.e. 89% of the total land-area of North Karelia) and peatlands (METLA 2011). Post-glacial esker and edge formations at 80–347 m a.s.l. are also typical, with sporadic small groundwater-fed natural ponds, where the species lives (Vuorio 2009). Biogeographically, the study area belongs mainly to the southern-boreal vegetation zone, as only the northern portion extends to the middle-boreal vegetation zone (Ahti *et al.* 1968). Nearly all forest lands in the study area

Survey methods

Before 2004, there were 31 known breeding ponds of the great crested newt in eastern Finland. During a LIFE Nature project “Protection of *Triturus cristatus* in Eastern Baltic Region”, 37 new breeding ponds were found in eastern Finland in 2004–2008 by means of dip-netting during the larval period (Briggs *et al.* 2006, Vuorio 2009). After the project, and 2009 dip-netting, there were 70 known breeding ponds (Vuorio 2009). In this study, we conducted a more detailed field survey focusing only on ponds with observed breeding. In the first step, the 70 breeding ponds were assigned to three groups of 23–24 ponds according to their average breeding success in 2005–2009. From each of these three groups, 15–16 ponds were randomly selected for more detailed data collection. The total number of selected ponds was 46.

In 2010–2011, the 46 selected ponds were re-surveyed and newt larvae were captured using dip-netting (Briggs *et al.* 2006, Skei *et al.* 2006, Skelly & Richardson 2010). A drop-shaped net was used to facilitate effective netting in ponds with floating vegetation. A standard dip-netting

method was to use a two-meter sweep at the shoreline. During the seven years (2005–2011) of data collection, each pond was visited on average 4.98 (\pm 0.27 SE) times. During a visit, the sweeping was repeated on average 28.4 (\pm 0.95 SE) times in each pond. Dip-netting was always done once per pond at the beginning of August. Numbers of sampled ponds per year varied from 21 to 46 due the fact that some ponds dried up and new breeding sites were found during the study.

As a rule, the entire pond was walked around and dip-netted at regular (2–4 m) intervals. In large ponds, sampling started from the sunny northern shore of the pond, where the larvae of the great crested newt were found more regularly. The breeding success is reported as the number of larvae caught per dip-net per pond per year. Because the proportion of the sampled area in the total pond area varied between ponds, the value for breeding success is not an explicit measure of the size of the larval population but an indicator of the overall breeding success in a pond.

Environmental predictor variables

The surroundings of the ponds within a radius of 100 m from the highest water level were classified into separate vegetation types and successional stage of forests according to mire- and forest-type classification systems (Eurola *et al.* 1995, Hotanen *et al.* 2008). The median size of separate patches of mire and forest stands was 2390 m² (range 102–55 113 m²), the median number of separate vegetation types per pond was nine. From this data, five variables reflecting quality of the habitat surrounding the studied pond were measured: (i) highest proportion of broad-leaved trees (older than 15 years) within a single forest stand, (ii) sum total area of forest stands of herb-rich vegetation (predominantly of the *Oxalis-Maianthemum* type), (iii) shade (angle between the water level and the tree tops, measured from the northern shore of the pond towards the south), (iv) total amount of unsuitable habitat patches (clearcuts, poorer forest types than *Myrtillus*-type, drained and nutrient-poor mires, roads, gravel pits and ponds with fish),

and (v) area of young forest stands (younger than or equal to 15 years). In addition, two variables, focal-pond area and the number of other small (< 5000 m²) ponds within a 500-m radius from the pond, reflecting the spatial population structure of the ponds in the study area, were measured from the basic maps. The measured variables, units, ranges and mean values used in the subsequent modeling are listed in Table 1.

Data analysis

We used generalized additive models (GAMs) to model the breeding success of the newt, by using calibrated breeding success as a response variable and the selected habitat characteristics as predictor variables. We applied the Gaussian probability distribution in GAM. GAMs are a non-parametric extension of generalized linear models (GLM). GAMs are especially useful for detecting and describing nonlinear species–environment relationships (Hastie & Tibshirani 1986, Austin 2002). Following Denoël and Lehmann (2006), GAMs were mainly performed via the user interface GRASP (Generalized Regression Analysis and Spatial Prediction, Lehmann *et al.* 2003) embedded in S-PLUS (ver. 6.1 for Windows, Insightful Corp.). Prior to modeling, the correlations between the seven candidate predictors were tested in order to detect inter-correlations (Table 2). However, as all these correlations were well below 0.8 (cf. Denoël & Ficetola 2008), all the environmental variables were employed in the model.

The GAMs were developed using a stepwise selection procedure (backward and forward) to find relevant explanatory variables. The default smoother degrees of freedom were set to three, to test for linear relationships, while the alternative smoother degrees of freedom were set to one. Variable dropping or conversion to linear form were tested by Akaike's Information Criterion (Akaike 1973). The goodness of fit of the models was assessed in two ways: (i) the explanatory power of the model evaluated by the proportion of explained deviance (D^2) of the total deviance in the model, and (ii) the predictive performance of the model evaluated by plotting the recorded newt abundance against predicted

abundances and calculating the Spearman correlations, based on a four-fold cross-validation (Denoël & Lehmann 2006, Parviainen *et al.* 2008). The contribution of each environmental variable to newt abundance was evaluated by an analysis of variance (ANOVA) in S-PLUS, and the two options provided in GRASP: the sole contribution (i.e. single or univariate model contribution) and the model contribution (i.e. the contribution of each predictor within the selected model, for more details see Lehmann *et al.* 2003, Denoël & Lehmann 2006).

Examination of residuals from the first model runs indicated that three ponds appeared to be

statistical outliers in the analysis (see Lehmann *et al.* 2003), and thus they were excluded from the final model building. The ultimate GAMs were generated in three main phases. First, we developed a GAM where we related newt abundance to the five habitat factors and the area of ponds in the pond surroundings using the step-wise procedure outlined above. Second, after developing this first GAM, we created two ecologically most reasonable interaction variables based on species ecology by multiplying (1) herb-rich forest by number of ponds, and (2) unsuitable habitats by young stands (cf. Crawley 2007). These two interactions were then entered

Table 1. Environmental variables included in modeling the abundance of juvenile great crested newts, rational for predictor variables, and measurement units and their range.

Variable	Reasoning	Min	Max	Average
Habitat variables				
Highest proportion (%) of broadleaved trees in a forest stand	Broadleaved trees provide leaf cover and decayed tree-trunks for hiding and hibernation	0	100	59.9
Herb-rich vegetation (ha) within a 100-m radius	Nutrient rich soil sustains more invertebrates to feed on	0	3.69	0.78
Shade (degrees) ^a	Shade keeps the ice cover longer on the ponds and water stays cooler during the summer, thus limiting the growth of larvae	7	37	18.7
Unsuitable habitats (ha) within a 100-m radius	These habitats do not provide good quality hibernation or feeding sites	0	4.09	0.84
Young stands (6–15 years after clear cutting) (ha) within a 100-m radius	This habitat does not provide good quality hiding or feeding sites	0	5.86	0.87
Spatial variables				
Number of small (< 5000 m ²) ponds within a 500-m radius from the pond shoreline	High number of ponds in the newt surroundings supports a larger local metapopulation	0	6	2.49
Focal-pond area (m ²)	Larger ponds support larger newt populations	74	3906	1215

^a An angle between the northern shore line and the top of the crown layer at the southern pond-edge.

Table 2. Spearman's correlation coefficients between the habitat and the pond area predictor variables. For details on the variables see Table 1.

	Pond size	Broad-leaved trees	Shade	Herb-rich vegetation	Unsuitable habitats	Number of small ponds
Broad-leaved trees	-0.204					
Shade	-0.612	0.183				
Herb-rich vegetation	-0.126	0.386	0.260			
Unsuitable habitats	0.101	-0.171	-0.395	-0.298		
Young stands	0.283	0.027	-0.217	-0.329	-0.062	
Number of small ponds	-0.227	-0.160	0.359	0.090	-0.376	-0.029

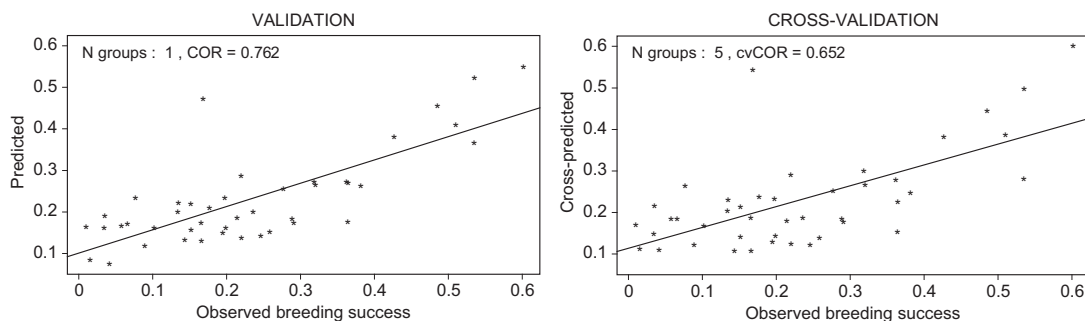


Fig. 2. Predicted reproductive success plotted against recorded values in simple re-substitution validation and four-fold cross-validation.

into the first GAM one at a time, and the difference in the goodness of fit of the models with and without the interaction terms were tested using ANOVA. In the third step, GAMs with only pond area, or number of ponds in the neighborhood, or both, were modeled. Finally, the performance of these GAMs and the first GAM were compared and tested with ANOVA (Crawley 2007).

In addition to field measurements, corresponding data for all five habitat variables could also be extracted from the databases of regional forest inventories governed by forestry authorities. Therefore, the statistical models developed in this study could be applied to surrounding regions in eastern Finland where no newt surveys have been conducted so far.

Results

The first GAM model used a stepwise variable selection process and AIC model selection criteria, and included all five habitat predictor variables (the number of small ponds in the surroundings was excluded during the stepwise process, and the pond area was not considered here). The inclusion of interaction terms ‘herb-rich forest \times number of ponds’ and ‘unsuitable habitats \times young stands’ did not provide statistically significant improvements to the model (ANOVA with F -test: $F_{4,00} = 2.130$, $p = 0.100$ and $F_{4,00} = 0.785$, $p = 0.544$, respectively), and thus the first GAM was kept as the final model.

Our final GAM explained more than half of the total deviance ($D^2 = 0.580$) in variation in newt breeding success. The correlation between

the recorded and fitted larval newt abundance values was notably high in the simple (re-substitution) validation ($r = 0.762$, see Lehmann *et al.* 2003), but somewhat lower in the four-fold cross-validation results ($r = 0.652$) (Fig. 2). Both the model contribution and single contribution statistics from GRASP showed that the main factor explaining breeding success was the area of herb-rich forests (Fig. 3). Subordinate contributions were related to the area of unsuitable habitats and shade (model contributions) and the highest proportion of broadleaved trees in a forest stand (single contribution). ANOVA of the successive inclusion of the variables into the final GAM highlighted the same two variables as the GRASP single contribution test (Table 3).

The response curves of the individual variables included in the final GAM differed in their shapes (Fig. 4). The relationship between the area of herb-rich forests and breeding success showed positive correlation from one hectare upwards, and the ponds with the highest breeding success were also correlated with the highest proportion of broad-leaved trees in a forest stand. In contrast, lower breeding success was associated with increases in shade, area of young forest stands and area of unsuitable habitats in the vicinity of the ponds.

GAMs including only the pond area, or the number of ponds in a 500-m radius, or both, explained only a very modest amount of the variation in newt breeding success (the percentages of the explained deviance (D^2) were 6.63, 8.31 and 14.16, respectively). Consequently, the final GAM with five habitat variables performed significantly better than the three GAMs with spatial variables ($F_{-4,04} = 10.566$, $p = 0.000096$,

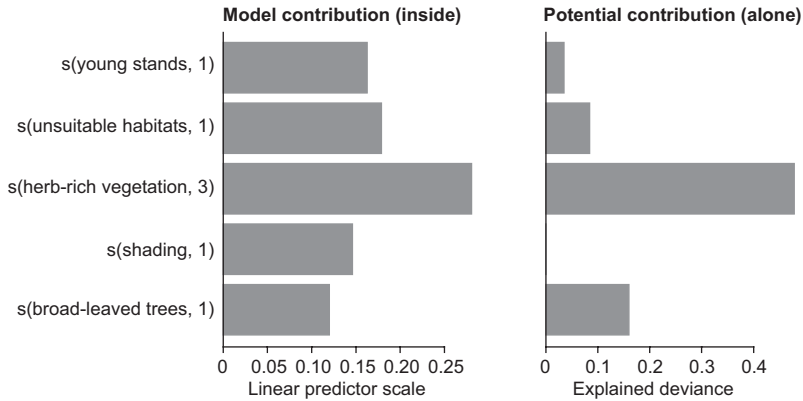


Fig. 3. Environmental variables included in the model of breeding success of the great crested newt. The extent of herb-rich forests is the most important variable both inside the model and when tested alone.

$F_{-4,04} = 10.220$, $p = 0.00013$, $F_{-1,04} = 39.94$, and $p = 0.0000075$, respectively).

Discussion

Factors affecting reproductive success

Gustafson *et al.* (2011) investigated local and landscape-scale habitat variables that affect quality of areas next to ponds, and occurrence patterns of the great crested newt in hemiboreal central Sweden. They concluded that in addition to pond-related abiotic and biotic factors (*see* Gustafson *et al.* 2009) adjacent terrestrial habitat characteristics also contribute significantly to the distribution of the newt, suggesting that suitable aquatic breeding sites and terrestrial environments should be addressed simultaneously (*see* also Denoël & Lehmann 2006, Denoël & Ficetola 2008). Abundance and proximity of deciduous forests had a positive impact on newt distribution, whereas coniferous forest had a negative effect (Gustafson *et al.* 2011).

Table 3. Analysis of variance (ANOVA) of the final GAM model, which tests the successive inclusion of variables into the model and shows the order in which variables were incorporated into the final GAM.

Variable	<i>F</i>	<i>p</i>
s(broadleaved trees, 1)	0.360	0.00025
s(shade, 1)	0.362	0.000095
s(herb-rich vegetation, 3)	3.545	0.0396
s(unsuitable habitats, 1)	0.451	0.0622
s(young stands, 1)	0.302	0.0418

Our results from the boreal vegetation zone are largely congruent with the conclusion of Gustafson *et al.* (2011). Moreover, straightforward and easy habitat inventories in the field or readily available terrestrial habitat data can provide useful variables for modeling the reproductive success of the great crested newt in boreal ponds. Areas of herb-rich, coniferous or mixed forests in the surroundings of a pond were the single most prominent explanatory variable for breeding success. In effect, herb-rich forests provide hiding places against predators, shelter against desiccation and an abundance of nutrition for great crested newts (Jehle & Arntzen 2000). Apparently, these factors improve the survival of individuals in the vicinity of the ponds and result in higher breeding populations in the ponds, in comparison with ponds that have other types of forests in their surroundings. Interestingly, the proximity of forests have been found to be critical for newt occupancy and maintenance of larger populations in central Europe (Denoël & Lehmann 2006, Denoël & Ficetola 2007, 2008). Herb-rich lush forests that provide cover for the newt on the shores of their breeding pond seem to be a general pattern across different biogeographical zones in Europe.

Ficetola and Denoël (2009) provided a useful example of how ecological thresholds in the relationships between response variables and environmental variables may be determined from GAM results. Similarly, an ecological threshold can be detected in our result. In our case, the shape of the response curve suggests that there is a threshold in the area of herb-rich forests, i.e. at approximately one ha. Below this, the area

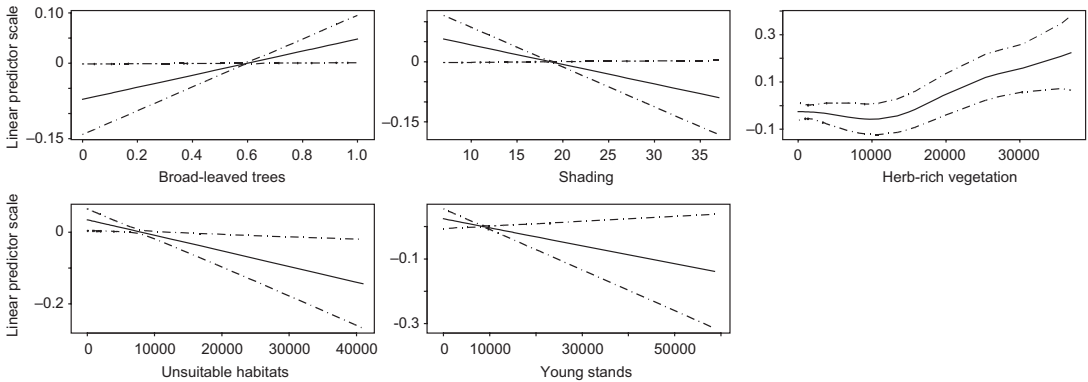


Fig. 4. Response curves of the breeding success of the great crested newt to the environmental variables selected by the generalized additive models.

of suitable terrestrial habitat starts to limit the breeding of the great crested newt. Apparently ponds with less than one ha of herb rich forest in their close vicinity are suboptimal environments for the great crested newt.

Based on the single (univariate) contributions of the predictor variables, the highest proportion of broad-leaved trees in a forest stand had the second highest and similar positive relationship with the great crested newt breeding success. This relationship may be because large amounts of broad-leaved deciduous trees provide plenty of leaf litter, which increases the soil pH and amount of nutrition and invertebrate prey items on the ground (Wareborn 1992, Ponge 2003), and thereby the number of adults and breeding activity. In contrast, young forest stands had a negative effect on breeding success. All the young forests at our study sites have originated from clear cuts or seed tree cuttings. Broad-leaved trees are regularly removed from these stands. Such forest management activities expose the habitat to increased solar radiation and more extreme air and soil temperatures, thus making the soil vulnerable to desiccation, causing changes in the fauna of the soil and field layer (Brosfoske *et al.* 1997, Jalonen & Vanha-Majamaa 2001, Siira-Pietikäinen & Haimi 2009, Work *et al.* 2010). These changes make young managed stands unattractive sites, characterized by a lack of moist and shaded ground, and scarcity of nutrition and hiding places. In some earlier studies, certain salamander species have also been shown to avoid open areas (Patrick *et al.* 2006). By and large, coniferous monocultures

probably provide a suboptimal terrestrial habitat for newt species in comparison to deciduous or mixed forests (Gustafson *et al.* 2011).

The total amount of unsuitable habitats appeared as the second most important habitat variable in the model. As expected, this compound variable was negatively related to breeding success. Interestingly, the importance of this effect became apparent only after the additive stacking of all unsuitable habitats; separately they did not show any statistical significance due to great variety and small surface areas of these habitats.

The effect of shade was negatively related to breeding success, but the lack of a direct univariate contribution suggests that its impact is subordinate to more prominent factors, and it operates mainly as an effect in a multivariate setting. Increased shade is mainly related to taller trees, and the ruggedness of the topography on the southern side of a pond. In addition, the size and shape of a pond affect how notable a shade effect is. In our study area, shady ponds remained ice-covered up to two weeks longer as compared with more open, sun exposed ponds (V. Vuorio unpubl. data). Such ponds remain cooler during the whole summer, which extends the larval phase (Duellman & Trueb 1986) and exposes the larvae to predation for longer periods than in sunnier ponds. During the most adverse years, larvae might not reach metamorphosis before the pond dries up or freezes over. Therefore, increased shade can translate into increased mortality of larvae and smaller adult cohorts.

Area and isolation of ponds

We investigated how the breeding success of the great crested newt can be explained with spatial variables commonly used in metapopulation studies, namely the area and isolation of a given pond, in comparison with terrestrial habitat factors. This question is of interest in conservation planning, both because a pond is the key element for the regeneration stage of the newt, and because area and isolation are variables which can be easily measured from existing maps for modeling purposes. Some earlier studies found that the number of (inhabited) ponds in the near vicinity may support the occupancy of amphibian populations (Denoël & Lehmann 2006), or that pond size may be used as a surrogate for patch quality (Piha *et al.* 2007), suggesting an underlying metapopulation structure in amphibians. Joly *et al.* (2001) studied the occupancy patterns of three newt species (*T. cristatus*, *T. helveticus* and *T. alpestris*) in France, and reported that the presence of these species was positively correlated with the number of other ponds within the 50 ha area surrounding the pond. However, other studies have shown contrasting results, and argued that the patch size and isolation are not necessarily intimately correlated with the level of critical resources (Pellet *et al.* 2007, Robles & Ciudad 2012).

Our results showed that the pond area and the number of all ponds, with or without great crested newts, within a radius of 500 m (reflecting the isolation of the pond) are poor predictors of the reproductive success of the great crested newt. This was particularly evident when comparing the amount of explained deviance: GAMs with pond area, isolation or both, explained four to five times less variation in breeding success than the GAM with the five habitat variables. Thus, it appears that pond area or isolation may not be reliable predictors of the best reproductive sites for the great crested newt in forest-dominated boreal landscapes. In a similar vein, Pellet *et al.* (2007) found that the connectivity of habitat patches had a surprisingly small effect on the colonization–extinction dynamics of amphibians. One potential reason for the absence of area or isolation effects is that established

populations of long-lived amphibians may be relatively stable as long as the habitat remains largely undisturbed. In such situations, extinction and colonization events do not become apparent within the short time-frame of most ecological research. Marsh and Trenham (2001) argued that the isolation effect of a pond may be strongest in areas where the surrounding terrestrial habitats are highly altered. Moreover, they suggested that isolation effects may actually be better explained by the distribution of terrestrial habitat than by the isolation of breeding ponds themselves. Their conclusion was that although the metapopulation design “ponds-as-patches” view is useful in many respects, it may be an oversimplification for many amphibian species, and thus should be applied with caution. The findings of the present study are concordant with the conclusions of Pellet *et al.* (2007) and Marsh and Trenham (2001), and suggest that the study area and corresponding forest-dominated boreal landscapes represent less disturbed environments for amphibians than the densely-populated central and southern European regions (cf. Joly *et al.* 2001).

Conclusions

Gustafson *et al.* (2011) concluded that the occurrence patterns of the great crested newt may be predicted by the terrestrial habitat characteristics of the surrounding landscape. We agree with this conclusion, and have shown here that the reproductive success of the newt species is also intimately related to habitat factors, in particular the abundance of herb-rich forests and deciduous trees. This is an important finding, because the presence–absence occurrence data do not necessarily predict the viability of a population in a patch, whereas ecologically the abundance of juvenile newts and the underlying environmental drivers may provide a useful basis for separating stable populations from declining ones, and predicting suitable locations for as yet undiscovered viable newt populations. Thus, models such as GAMs may be used as a basis for regional conservation planning of the great crested newt. Practical methods are needed, since intensive forest management practices, which create open

areas and favor coniferous monocultures in the vicinity of ponds, diminish the quality of breeding ponds and their surroundings (Patrick *et al.* 2006, Gustafson *et al.* 2011). Using models that employ habitat variables derived from a landscape, it is possible to locate potential new breeding sites and target fieldwork effectively. Further, the models and their predictions can be revised using empirical data on critical pond-related factors sampled from identified locations.

It is imperative to acknowledge that recommendations for species conservation measures can be outlined using models that utilize compositional variables of the surrounding landscape. Thus, the results shown here provide the first guidelines for determining potential sites for conservation of the great crested newt in the boreal forest landscape. Based on our results, construction of new artificial ponds can be targeted to the most promising sites. Artificial ponds have been found to be an effective method to mitigate the negative impacts of human activity upon many amphibian species, including the great crested newt (Rannap *et al.* 2009). Our results corroborate earlier recommendations to coordinate the management planning of both aquatic and terrestrial habitats when aiming at successful conservation of amphibian species (Denoël & Lehmann 2006, Gustafson *et al.* 2011). For the great crested newt in boreal forests, this means that conservation of the breeding ponds alone is not sufficient, but forestry practices in the vicinity of the ponds also need to be adjusted so the species and its habitat are maintained. In practice, this means that herb-rich forests in the vicinity of ponds should be preserved and deciduous trees should be favored in other forest types, so that forest management should not result in open, sunny forest floors and loss of food resources and hiding places for the great crested newt.

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