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Terrestrial habitat predicts use of aquatic habitat for breeding purposes — a study on the great crested newt (*Triturus cristatus*)

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This study examines the structure and composition of landscapes surrounding ponds with and without great crested newts (*Triturus cristatus*) — a species that needs an aquatic and a terrestrial environment. We related presence and absence data to 31 local and landscape variables, in a total of 143 areas in south-central Sweden. Land-use variables were measured within the radii of 100 m (local scale) and 500 m (landscape scale) surrounding the ponds. To find drivers of the distribution of great crested newts we used a principal component analysis (PCA) and a logistic regression analysis. Higher amounts of deciduous forest and pasture, together with proximity to deciduous forest seem to be positive for presence of great crested newts. Coniferous forest and mire appear to have a negative effect on the habitat quality for the species. We argue that management of the great crested newt should to a greater extent include the terrestrial habitat. Special attention should also be given to identifying and securing older, deciduous-rich forest in the vicinity of breeding ponds.

Introduction

The successful management of landscapes for species dependent on several different environments is a great challenge for conservation research and practice (e.g. Law & Dickman 1998, Sergio *et al*. 2003). In the case of semi-aquatic organisms like many amphibians, the issue of providing a landscape with a combination of suitable aquatic breeding sites (e.g. ponds) and favourable terrestrial habitats is particularly important (e.g., Semlitsch 1998). The decline of landscape heterogeneity, linked to e.g. intensified agriculture and forestry practices, is making many contemporary landscapes less suitable for such species (Beja & Alcazar 2003, Garcia-Muñoz *et al*. 2010).

An amphibian species that is dependent on different environments and, therefore, susceptible to changes in the landscape is the great crested newt (*Triturus cristatus*, Salamandridae). This caudate is distributed throughout central and eastern Europe and the western part of Russia; an area that is densely populated and has been affected by human influence for thousands of years (Kuzmin 1994, Griffiths 1996, Gasc *et al*. 1997). Typical aquatic and terrestrial newt habitats (i.e. ponds and low-intensive mixed agricultural and semi forested landscapes) are both among those that have generally decreased through modern land use (Bernes 1994, Ihse 1995, Hull 1997, Benton *et al*. 2003). Thus, it is assumed that the decline of landscape complexity through habitat loss is the largest single reason for decreasing populations of the species (Griffiths *et al*. 1996, Oldham & Swan 1997, Langton *et al*. 2001). A number of surveys have shown that several previously known great crested newt localities were destroyed during the 20th century (Beebee & Griffiths 2000, Edgar & Bird 2006, Malmgren 2007).

In landscapes inhabited by great crested newts and several other amphibian species, the aquatic and terrestrial habitats constitute distinct and equally essential landscape elements. Consequently, the amount of both elements must be sufficient and the habitats have to be adjoining or interconnected in some way to make movements between them possible.

The aquatic habitat of the great crested newt is essential for breeding and larval development (Griffiths 1996, Thiesmeier & Kupfer 2000). Several factors are of importance when characterizing an aquatic habitat. These include physical, chemical and biological characteristics, but also spatial considerations (e.g. their juxtaposition in the landscape) (Angelibért *et al*. 2004, Biggs *et al*. 2005, Scheffer & van Geest 2006, Gustafson *et al*. 2009, Hartel *et al*. 2010b). However, physio-chemical variables describing water quality usually have low relevance as compared with ecological variables that explain newt distribution on a more macroscopic level (Cooke & Frazer 1976, Beebee 1985, Pavignano *et al*. 1990, Ildos & Ancona 1994, Joly *et al*. 2001). A typical habitat for the great crested newt seems to be a moderately shallow pond, small lake or tarn that holds abundant vegetation and a diverse invertebrate fauna (Swan & Oldham 1993, Oldham *et al*. 2000, Thiesmeier & Kupfer 2000, Sztatecsny *et al*. 2004, Gustafson *et al*. 2006, Denoël & Ficetola 2008). On land, the great crested newt requires a habitat that provides protection from desiccation and predators, as well as foraging opportunities, during post-breeding period and juvenile dispersal (Griffiths 1996, Thiesmeier & Kupfer 2000, Langton *et al*. 2001, Malmgren *et al*. 2007). The terrestrial habitat must contain areas for refuge during more extreme weather conditions, and allow for hibernation during winter. Studies on the terrestrial ecology of the species are scarce but indicate that preferred habitats include forests, woodlands and old pastures (Griffiths 1996, Latham & Oldham 1996, Jehle & Arntzen 2000, Joly *et al*. 2001, Langton *et al*. 2001). The great crested newt seems to favour an area directly adjacent to a breeding pond or within a few hundred meters from the pond as a terrestrial habitat (Dolmen 1982, Latham & Oldham 1996, Baker & Halliday 1999, Jehle 2000, Oldham & Humphries 2000, Malmgren 2002). However, different types of land use and vegetation are probably important on different spatial scales and distances from an aquatic habitat (Ficetola *et al*. 2009). Moreover, characteristics of the terrestrial habitat of the great crested newt may vary considerably in different parts of the geographic range of the species.

Some types of environments are actively avoided by great crested newts. These include ponds occupied by predatory fish (Cooke & Frazer 1976, Thiesmeier & Kupfer 2000, Malmgren 2001) and open fields with limited vegetation (Jehle & Arntzen 2000, Oldham *et al*. 2000, Joly *et al*. 2001, Malmgren 2002). Other environments, such as roads and similar man-made structures, are probably not actively avoided but cause increased mortality (Hels & Buchwald 2001, Fahrig & Rytwinski 2009). The remaining landscape is supposedly neutral and may be used for migration. To sustain viable populations of the great crested newt, there must be numerous existing and potential aquatic habitats and abundant terrestrial habitat, with interconnecting corridors and within migration distance, in a so called "pondscape" (Swan & Oldham 1993, Jehle 2000, Joly *et al*. 2001, Langton *et al*. 2001, Malmgren 2002).

Several authors (e.g. Vos & Stumpel 1995, Vos & Chardon 1998, Marsh & Trenham 2001, Ficetola & De Bernardi 2004, Denoël & Lehmann 2006) emphasized the importance for amphibians of both the terrestrial habitat and the landscape structure, and suggested that a larger scale approach could better explain observed patterns. To our knowledge, there are no published studies that examine the link between aquatic and terrestrial habitats of great crested newts in Fennoscandia. We assume that the landscapes in this region, with generally higher forest cover and harsher climate than in the rest of Europe, largely influence this relationship and new knowledge may be of great importance for conservation of the species. The purpose of this study was, thus, to test if the compositional differences in landscapes surrounding ponds can predict the patterns of occurrence of the great crested newt at the northern edge of the species distribution range. We use two important pond variables (presence of predators and size of ponds), one regional variable (altitude), and 15 variables describing the landscape surrounding potential breeding ponds to explain the use of ponds as aquatic habitats. We also examine if patterns of landscape composition are scale-dependent. The terrestrial environment is defined on a "local" scale, within 100 m, and on a broader "landscape" scale within 500 m from the aquatic habitat. Our aim was to analyze what lies behind observed patterns of newt occurrence in the field, and to provide useful information on how to manage and conserve species that are dependent on both aquatic and terrestrial habitats in heterogeneous landscapes.

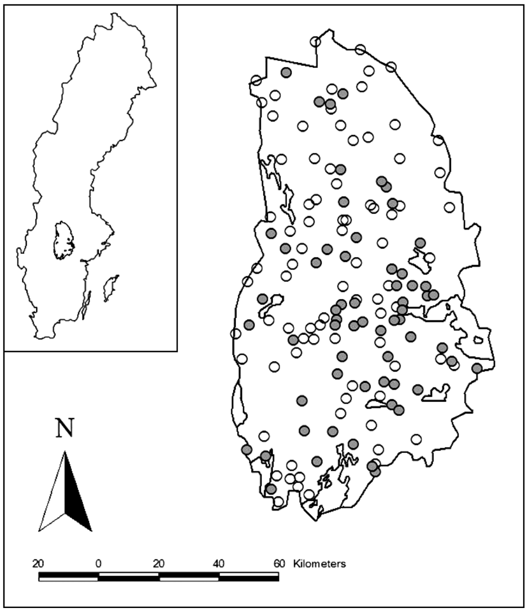

Fig. 1. Locations of studied ponds with presence (grey circles) and absence (open circles) of great crested newts within the Örebro County. The map in the upper left corner shows the general location of the Örebro County in Sweden.

Material and methods

Study area

The study is based on a survey of great crested newts that was performed in the Örebro County in 2003 by the Örebro County Administrative Board (Hellberg *et al*. 2004). The Örebro County covers an area of approximately 9300 km^2 in south-central Sweden (Fig. 1). The bedrock of the northern, southern and western parts of the county is mainly granite of the Scandinavian Shield. Here, the elevation varies between 50 and 400 meters above sea level (in approximately 80% of the county area) (Fig. 2). In the central eastern part of the county the bedrock is mainly sedimentary and Cambro–Silurian, with sand-, lime- and clay stone. The elevation here is between 20 and 100 meters above sea level (approximately 20% of the county area).

The central-eastern part is the most densely populated, and the land use is dominated by large-scale agriculture, with fragmented remains of small-scale farmland with natural pastures (Fig. 3). The forests in this part are mainly coniferous (*Picea abies*, *Pinus sylvestris*), but contain larger admixture of deciduous trees (mainly *Populus tremula*, *Betula pubescens*, *B. pendula*, *Alnus glutinosa*, *Sorbus aucuparia*) than in the rest of the county. Hardwood species (e.g. *Ulmus glabra*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*) are rare and generally occur only in pockets on slopes and in the lowland. The northern, southern and western parts of the county are less populated and dominated by coniferous forests with extensive forestry (Fig. 3). Small scale agriculture is

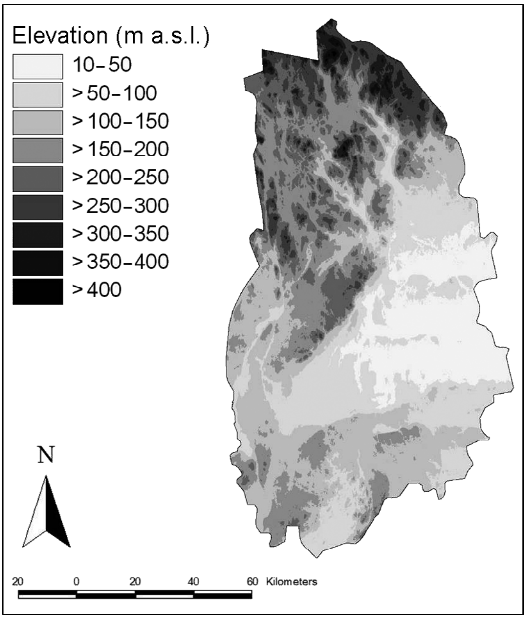

Fig. 2. Topography of the Örebro County.

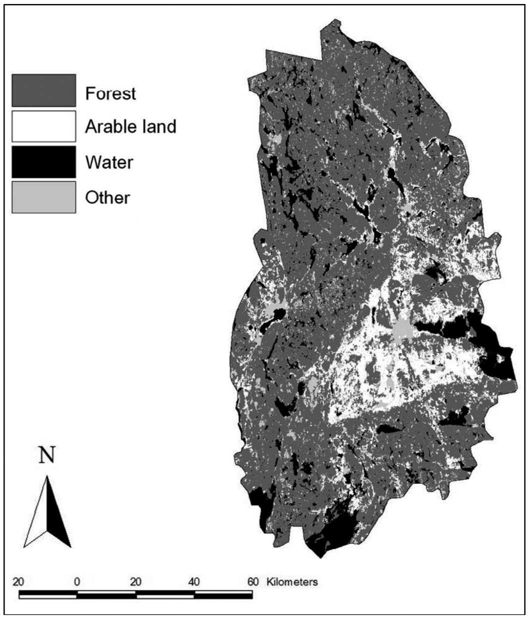

Fig. 3. Land categories in the Örebro County.

also present. The division between higher and lower elevation areas in the county is sharp and in part consists of escarpments. This sharp division brings a well-defined limit in climate and temperatures. The "*Limes Norrlandicus*", which runs across the central regions of the Örebro County, represents the northern distribution limit for many nemoral or hemiboreal species, and the southern limit for many boreal species.

The survey — data and field methods

The main rationale behind the great crested newt survey in 2003 was to investigate the distribution of the species and to locate areas with presence of great crested newts for conservation purposes (Hellberg *et al*. 2004). The aim was to survey one area in every 2 × 2 km square in the county, which resulted in a total count of 530 surveyed ponds in 134 areas separated by at least 1 km. The survey method used was standardized visual observation (torching) (Griffiths *et al*. 1996, Langton *et al*. 2001, Malmgren *et al*. 2005). Ponds were surveyed during at least two different nights in May and June, except when newts were found already during the first visit. Great crested newts were found in 86 ponds in 52 separate areas. In the remaining 82 areas, the species was not confirmed. To avoid overlap between ponds in the landscape analyses, we randomly selected one pond from every surveyed area. If there were ponds with presence of great crested newts in an area, we selected these prior to ponds with absence. We also included randomly selected ponds from nine additional areas with presence of great crested newts, which were surveyed in 2002 using the same method. In total, 82 ponds without and 61 ponds with great crested newts were included in the study (Fig. 1).

Explanatory variables

Most of the explanatory variables that describe land use and vegetation in the area surrounding the ponds were derived from the Swedish CORINE land-cover data (Lantmäteriverket 2002). This country-wide database describes 57 different types of land cover and has been produced mainly from satellite images (Landsat TM) acquired around the year 2000, that were combined with the existing topographic maps. The minimum area of objects mapped in Swedish CORINE is 1 ha. In our analysis, we used a vector-based version of these data.

Additionally, we used two other variables concerning older forest habitats of potential importance as terrestrial habitat for the great crested newt. Old deciduous forest was defined as a forest that contains at least 25% deciduous trees by timber volume and is older than 60 years. Old coniferous forest was defined as a forest with at least 50% coniferous trees by timber volume and older than 80 years. Age of forest and amount of deciduous and coniferous trees was based on estimates of forest variables produced by the Swedish University of Agricultural Sciences (SLU) in 2003 (Reese *et al.* 2003). These data were obtained by combining remote sensing information from Landsat 7 ETM satellite imagery (from 1999 and 2000) with field data from a separate set of Global Positioning System (GPS) located plots from the National Forest Inventory (NFI) using the k-nearest neighbor (kNN) method (Reese *et al.* 2003).

Land use in the neighbourhood of the ponds was measured and analyzed at two different scales: within radii of 100 m (local scale) and 500 m (landscape scale). The area of the pond was excluded when measuring the amounts of different land use types within the buffer zone. Distances from pond coordinates to closest forest and deciduous forest were measured and also included in the study. Two local variables concerning ponds were considered: pond size and presence of predatory fish and/or crayfish. No other pond variables were collected during the field study, as the survey was conducted during night and no extra visits were possible due to economic limitations. We also included elevation, defined as meters above sea level at the pond coordinate and calculated in GIS from the Digital Elevation Model (Lantmäteriverket 2010). Percentages of different land-use types, distance to forests and elevation were calculated using ArcView 3.2 with the X-Tools extension (ESRI 2001). Pond size and presence of fish and/or crayfish were based on estimations or field observations.

Data analyses

Initially, the two groups of ponds (with newts and without newts) were compared using a two-sample *t*-test, for each of the 31 variables. To reduce the number of variables and to avoid multicolinearity among explanatory variables in the following logistic regression analysis, we used principal component analysis (PCA). Prior to the analysis all data were $\log(x + 1)$-transformed (Zar 1999). The first 12 principal components were selected for further analyses, based on eigenvalues (> 0.7) and the shape of scree plots (Everitt & Dunn 2001). We interpreted the association between the 12 axes and the original variables using the broken-stick criterion (Jackson 1993, Peres-Neto *et al.* 2003). To examine the relative importance of the different variables on the distribution of great crested newts we examined the relationship between the derived principal components and the two groups of ponds (with newts and without newts) using a logistic regression with a backward successive exclusion of variables. Model significance was evaluated with a likelihood ratio test (Hosmer & Lemeshow, 2000). Models were compared and ranked using Akaike's Information Criterion (AIC; Burnham & Anderson 2002, Mazerolle 2006), and we calculated AIC_c to account for low sample size (Burnham and Anderson 2002). The model with the lowest AIC_c value is the one best supported by the data. The difference in AIC_c between the model *i* and the model with the lowest AIC_c value describes the relative importance of the different models ($AIC_{ci} - AIC_{c\_min} = \Delta_i$). All models with $\Delta_i < 2$ can be considered equal in making inferences (Burnham & Anderson 2002). We also calculated Akaike weights (w_i), to determine the strength of evidence for each model (Burnham & Anderson 2002).

Results

For 15 out of the measured 31 variables, there were significant differences between ponds with and without great crested newts (Table 1). The principal component analysis resulted in 12 components whose eigenvalue exceeded 0.7 (Table 2). Together the 12 components explained more than 82.7% of the variance. The first component explained 21.1% of the variance, and was positively associated with elevation, coniferous forest, mire and distance to deciduous forest. There was

Table 1. Group means, standard error and range for pond and landscape variables on a sample of 143 ponds from south–central Sweden where great crested newts (*Triturus cristatus*) were either present or absent. Univariate comparisons of the two pond groups with a *t*-test for independent samples are presented; *p* values indicating significant differences are set in boldface.

Variable (name) (n = 31)	With newts (n = 61)		Without newts (n = 82)		t	p
	Mean ± SE	Min–Max	Mean ± SE	Min–Max		
Elevation (elevation) (m a.s.l.)	108.26 ± 7.99	24–267	156.01 ± 7.53	28–310	4.29	< **0.001**
Pond size (size) (m^2)	872.00 ± 139.65	10–4324.94	1317.95 ± 197.65	10–9540.15	1.72	0.087
Presence of predators (predation) (1/0)	0.0490 ± 0.0280	0–1	0.1700 ± 0.0420	0–1	2.24	**0.026**
Built up area 100m (built_100m) (proportion)	0.0084 ± 0.0065	0–0.38	0.0097 ± 0.0063	0–0.48	0.14	0.900
Built up area 500m (built_500m) (proportion)	0.0152 ± 0.0056	0–0.20	0.0102 ± 0.0043	0–0.30	–0.72	0.475
Garden and park 100m (park_100m) (proportion)	0.1240 ± 0.0343	0–1.00	0.1046 ± 0.0296	0–1.00	–0.43	0.668
Garden and park 500m (park_500m) (proportion)	0.0651 ± 0.0138	0–0.46	0.0539 ± 0.0141	0–0.58	–0.55	0.581
Field 100m (field_100m) (proportion)	0.0797 ± 0.0219	0–0.73	0.0359 ± 0.0135	0–0.71	–1.78	0.077
Field 500m (field_500m) (proportion)	0.1712 ± 0.0281	0–0.89	0.0662 ± 0.0148	0–0.73	–3.54	**0.001**
Pasture 100m (pasture_100m) (proportion)	0.1557 ± 0.0297	0–0.93	0.0449 ± 0.0117	0–0.61	–3.83	< **0.001**
Pasture 500m (pasture_500m) (proportion)	0.0861 ± 0.0144	0–0.57	0.0293 ± 0.0044	0–0.18	–4.24	< **0.001**
Deciduous forest 100m (dec_100m) (proportion)	0.1133 ± 0.0228	0–0.77	0.0561 ± 0.0129	0–0.58	–2.31	**0.022**
Deciduous forest 500m (dec_500m) (proportion)	0.0913 ± 0.0133	0–0.51	0.0466 ± 0.0073	0–0.35	–3.13	**0.002**
Old deciduous 100m (dec_old_100m) (proportion)	0.0112 ± 0.0040	0–0.23	0.0047 ± 0.0014	0–0.06	–1.69	0.093
Old deciduous 500m (dec_old_500m) (proportion)	0.0080 ± 0.0012	0–0.04	0.0048 ± 0.0006	0–0.03	–2.84	**0.005**
Mixed forest 100m (mix_100m) (proportion)	0.0849 ± 0.0140	0–0.57	0.0761 ± 0.0103	0–0.42	–0.52	0.606
Mixed forest 500m (mix_500m) (proportion)	0.0701 ± 0.0068	0–0.20	0.0755 ± 0.0049	0–0.21	0.66	0.509
Coniferous forest 100m (con_100m) (proportion)	0.1952 ± 0.0309	0–0.85	0.3115 ± 0.0351	0–1.00	2.39	**0.018**
Coniferous forest 500m (con_500m) (proportion)	0.2804 ± 0.0271	0–0.76	0.3759 ± 0.0240	0–0.84	2.63	**0.010**
Old coniferous 100m (con_old_100m) (proportion)	0.0478 ± 0.0118	0–0.36	0.0739 ± 0.0162	0–0.82	1.22	0.225
Old coniferous 500m (con_old_500m) (proportion)	0.0750 ± 0.0124	0–0.41	0.1036 ± 0.0120	0–0.53	1.63	0.105
Clear cut 100m (clear_100m) (proportion)	0.1794 ± 0.0240	0–0.93	0.1273 ± 0.0184	0–0.75	–1.76	0.081
Clear cut 500m (clear_500m) (proportion)	0.1620 ± 0.0124	0–0.49	0.1808 ± 0.0124	0–0.51	1.05	0.294
Mire 100m (mire_100m) (proportion)	0.0547 ± 0.0179	0–0.53	0.2042 ± 0.0341	0–1.00	3.52	**0.001**
Mire 500m (mire_500m) (proportion)	0.0334 ± 0.0079	0–0.34	0.1121 ± 0.0170	0–0.59	3.77	< **0.001**
Wetland 100m (wet_100m) (proportion)	0	0	0	0	–	–
Wetland 500m (wet_500m) (proportion)	0.0056 ± 0.0038	0–0.20	0.0011 ± 0.0009	0–0.07	–1.33	0.187
Lake and river 100m (lake_100m) (proportion)	0.0252 ± 0.0054	0–0.18	0.0675 ± 0.0125	0–0.55	2.77	**0.006**
Lake and river 500m (lake_500m) (proportion)	0.0156 ± 0.0036	0–0.15	0.0450 ± 0.0111	0–0.75	2.22	**0.028**
Distance to forest (dist_for) (m)	24.70 ± 6.89	0–299.98	171.71 ± 86.91	0–5793.75	1.46	0.148
Distance to deciduous (dist_dec) (m)	2500.50 ± 383.21	0–18353.48	3869.88 ± 375.86	0–14523.22	2.50	**0.013**

a negative association with predators, park and garden, field, pasture and deciduous forest within 500 m. The second component explained another 13.1% of the variation, and was positively associated with variables connected with deciduous or mixed forest, and negatively associated with distance to deciduous and other forest. The last three steps of the logistic regression may be considered equal in making inferences ($\Delta_i < 2$; Table 3). The best model according to Akaike's test was the last step (step 9), including principal components 1, 2, 4 and 12. This model had the lowest AIC_c and Δ_i and the highest Akaike weight (w_i).

Discussion

Our results suggest that the composition of the landscape and the amount of available terrestrial habitat are important features in predicting the distribution of great crested newts in their aquatic habitat. The distinction between areas with and without great crested newts could best be explained by a combination of four different principal components. In the first component, elevation is positively associated with amount of coniferous forest and mire and negatively associated with for example field and pasture. The

Table 2. Multivariate loadings of all included variables from principal component analysis for components 1 to 12. Values set in boldface indicate significant associations with the axes. The table also shows eigenvalue, variance (%) and cumulated variance (%) for the 12 components.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12
Elevation	**0.801**	0.061	0.186	0.229	0.039	–0.037	–0.041	0.102	0.017	0.103	–0.115	–0.165
Size	0.008	–0.373	0.171	0.319	0.090	0.333	–0.041	**0.290**	–0.101	0.390	**0.234**	0.291
Predators	**–0.265**	–0.167	–0.115	0.319	0.062	0.400	0.157	0.023	–0.058	0.332	0.317	–0.452
Built_100	–0.123	–0.021	–0.161	0.243	0.324	–0.024	0.278	0.405	**0.550**	–0.322	0.014	0.000
Built_500	–0.353	–0.176	–0.435	0.416	0.193	–0.004	0.197	0.121	0.299	–0.173	0.163	0.074
Park_100	**–0.492**	–0.202	**–0.532**	**0.385**	–0.039	–0.238	–0.117	–0.084	–0.258	0.145	–0.161	0.072
Park_500	**–0.540**	–0.219	**–0.536**	**0.415**	–0.038	–0.172	–0.087	–0.085	–0.107	0.095	–0.038	0.083
Field_100	**–0.423**	–0.163	0.091	**–0.512**	0.049	0.065	**–0.438**	0.099	0.220	0.112	0.168	–0.180
Field_500	**–0.707**	–0.161	0.032	**–0.453**	0.065	0.029	–0.348	0.066	0.038	–0.002	0.171	0.022
Pasture_100	**–0.558**	–0.009	0.178	–0.418	–0.087	0.137	0.364	0.061	0.218	0.215	–0.199	0.026
Pasture_500	**–0.665**	0.046	0.177	–0.237	–0.197	0.135	**0.423**	–0.117	0.074	0.057	–0.149	0.174
Dec_100	–0.353	**0.606**	0.374	0.211	–0.026	0.089	0.043	0.125	–0.145	–0.177	0.184	0.059
Dec_500	**–0.486**	**0.608**	0.245	0.204	–0.097	–0.061	–0.092	0.297	–0.089	–0.018	–0.161	–0.088
Dec_old_100	–0.072	**0.514**	0.217	0.248	–0.205	–0.001	–0.086	–0.217	0.186	0.028	0.346	0.412
Dec_old_500	–0.117	**0.731**	0.115	0.202	–0.194	–0.114	–0.170	0.303	0.043	0.128	–0.218	–0.027
Mix_100	0.249	**0.560**	0.071	0.132	0.125	0.009	–0.093	**–0.443**	0.310	0.238	0.184	0.119
Mix_500	0.408	**0.607**	–0.083	0.163	0.206	–0.081	0.066	–0.069	0.251	0.301	–0.183	–0.159
Con_100	**0.701**	0.233	–0.362	–0.175	–0.290	0.205	0.009	0.017	0.044	–0.004	0.016	–0.026
Con_500	**0.843**	0.213	–0.184	–0.125	–0.102	0.041	0.106	0.093	0.051	0.071	0.075	–0.110
Con_old_100	**0.550**	0.052	–0.360	–0.230	–0.315	0.155	0.080	0.307	–0.119	–0.004	0.026	0.256
Con_old_500	**0.735**	–0.045	–0.180	–0.188	–0.204	0.020	0.121	0.281	–0.116	0.009	0.201	0.151
Clear_100	0.065	0.187	0.079	–0.200	**0.760**	0.197	0.106	0.034	–0.261	–0.186	0.075	0.049
Clear_500	0.327	0.167	0.164	0.028	**0.653**	0.100	0.137	–0.064	–0.330	0.093	–0.160	0.168
Lake_100	0.180	–0.355	0.264	0.360	–0.078	**0.611**	–0.212	0.096	0.092	–0.043	–0.123	–0.092
Lake_500	0.157	–0.223	0.137	0.301	–0.237	**0.561**	–0.215	–0.287	0.061	–0.338	–0.275	0.089
Mire_100	**0.422**	**0.513**	**0.496**	0.225	–0.091	**–0.396**	0.063	0.014	–0.031	–0.021	0.110	–0.031
Mire_500	**0.449**	–0.452	**0.447**	0.149	–0.086	**–0.434**	0.038	–0.061	0.037	–0.135	0.133	–0.100
Wet_500	–0.216	–0.090	0.093	0.024	–0.294	0.114	**0.613**	–0.286	–0.121	0.008	0.086	–0.150
Dist_for	–0.066	**–0.584**	0.362	0.068	0.004	–0.120	0.083	0.256	0.138	0.311	–0.231	0.225
Dist_dec	**0.514**	**–0.445**	–0.166	–0.177	0.283	0.017	–0.091	–0.241	0.291	0.126	–0.143	0.134
Eigenvalue	6.336	3.920	2.268	2.243	1.843	1.609	1.399	1.252	1.152	0.991	0.916	0.869
Variance (%)	21.12	13.07	7.561	7.475	6.143	5.364	4.663	4.175	3.841	3.302	3.054	2.896
Cumulated (%)	21.12	34.19	41.75	49.22	55.37	60.73	65.39	69.57	73.41	76.71	79.77	82.66

second component is significantly associated with variables connected to amount of deciduous trees and proximity to forest. Higher amounts of deciduous forest and pasture, together with closeness to forest seem to be positive for presence of great crested newts. Coniferous forest and mire appear to have a negative effect on the habitat quality for the species. These findings confirm the assumption that deciduous forest and pastures are preferably used as terrestrial habitat by the great crested newt and that coniferous forest is suboptimal as terrestrial habitat for the species (Griffiths 1996, Latham & Oldham 1996, Jehle & Arntzen 2000, Thiesmeier & Kupfer 2000, Malmgren 2007).

As expected, the proportions of deciduous forest and pastures were generally higher in areas where the great crested newt was present. Furthermore, the results indicate that the amounts of deciduous forest and pastures are important both at local and landscape scales. The proximity of breeding ponds to deciduous forests had a strong positive effect. Deciduous forest probably create better microclimate than coniferous forest, with a moist and shaded ground layer and a greater abundance of leaf litter (Jehle & Arntzen 2000). The importance of low-intensity-use pastures to amphibians and species diversity in general is probably manifold (Tucker 1992, Jehle 2000, Sztatecsny *et al.* 2004, Kivinen *et al.* 2008, Hartel *et al.* 2010a). Pastures frequently contain a variety of microhabitats ranging in microclimate. Furthermore, the use of chemicals

Table 3. Results from logistic regression analysis with backward stepwise exclusion of variables (SPSS ver. 14.0). Twelve variables, that are the twelve first components from the principal component analysis in Table 2, were included in the initial step. The last four steps of the regression are presented in the table. Models are compared using Δ_i and Akaike weights (w_i); significant test values and p values indicating significances are set in boldface.

Model	B	SE	Wald's statistic	p		
Step 6						
Constant	–0.459	0.216	4.498	**0.034**	Nagelkerke R^2 = **0.377**	Δ_i = **3.330**
PC1	–0.954	0.226	17.77	< **0.001**	Hosmer-Lemeshow test = **0.109**	w_i = **0.0742**
PC2	0.777	0.238	10.70	**0.001**	Model p < **0.001**	
PC3	–0.112	0.225	0.246	0.620	–2log(likelihood) = **148.0**	
PC4	–0.768	0.247	9.655	**0.002**	AIC_c = **165.1**	
PC6	–0.292	0.284	1.056	0.304		
PC7	0.348	0.244	2.030	0.154		
PC12	0.621	0.234	7.043	**0.008**		
Step 7						
Constant	–0.434	0.209	4.319	**0.038**	Nagelkerke R^2 = **0.376**	Δ_i = **1.333**
PC1	–0.943	0.225	17.61	< **0.001**	Hosmer-Lemeshow test = **0.186**	w_i = **0.2014**
PC2	0.762	0.235	10.51	**0.001**	Model p < **0.001**	
PC4	–0.757	0.249	9.263	**0.002**	–2log(likelihood) = **148.2**	
PC6	–0.302	0.281	1.161	0.281	AIC_c = **163.1**	
PC7	0.344	0.246	1.955	0.162		
PC12	0.630	0.236	7.114	**0.008**		
Step 8						
Constant	–0.406	0.205	3.929	**0.047**	Nagelkerke R^2 = **0.367**	Δ_i = **0.3322**
PC1	–0.936	0.225	17.28	< **0.001**	Hosmer-Lemeshow test = **0.467**	w_i = **0.3322**
PC2	0.738	0.232	10.10	**0.001**	Model p < **0.001**	
PC4	–0.690	0.231	8.927	**0.003**	–2log(likelihood) = **149.4**	
PC7	0.318	0.254	1.566	0.211	AIC_c = **162.1**	
PC12	0.584	0.226	6.669	**0.010**		
Step 9						
Constant	–0.406	0.203	4.009	**0.045**	Nagelkerke R^2 = **0.355**	Δ_i = **0**
PC1	–0.880	0.210	17.59	< **0.001**	Hosmer-Lemeshow test = **0.479**	w_i = **0.3922**
PC2	0.721	0.231	9.744	**0.002**	Model p < **0.001**	
PC4	–0.641	0.227	7.946	**0.005**	–2log(likelihood) = **151.3**	
PC12	0.575	0.224	6.622	**0.010**	AIC_c = **161.7**	

and fertilizers is much lower in pastures than in agricultural fields. Low-intensity-use pastures can therefore be considered productive diversity hotspots in modern landscapes, and are also in many cases remains from the time when the landscape was more variable and managed at a smaller scale. Therefore, not surprisingly, our results clearly show that such landscapes are preferred by the great crested newt over intensively-managed landscapes dominated by agricultural fields and/or coniferous forests.

The positive association between presence of newts and amount of fields, pastures and deciduous forest within 500 m may be, to some degree, explained by climatic and geographic reasons. Larger amount of fields around ponds with newts was unexpected since fields are usually seen as a negative factor (Swan & Oldham 1993, Werner & Glennemeier 1999, Oldham *et al.* 2000, Joly *et al.* 2001). In the study area, the division between higher and lower elevation is relatively distinct, with fertile plains, large agricultural areas and a higher content of deciduous trees at lower elevations and mostly forested landscapes with coniferous trees at higher elevations. This division was also indicated by principal component 1. However, even if Örebro county lies close to the northern distribution limit of the great crested newt, the distribution of the species stretches over the whole study area and the species may still be found further north and at higher elevations (Dolmen 1982, Gasc *et al.* 1997, Malmgren 2007). The negative association between elevation and presence of great crested newts is possibly due to a combination of climatic factors and landscapes containing smaller amounts of adequate aquatic and terrestrial habitats. Great crested newts may prefer a mix of features, usually found in productive lowland landscapes also suitable for crop cultivation (Swan & Oldham 1993). In a study by Joly *et al.* (2001), the relationship between land occupied by cultivated fields and abundance of great crested newts was bell-shaped, which might suggest that the newt abundance within a pond is higher in landscapes where the proportion of area in cultivation is moderate. Terrestrial habitat features are probably more important in landscapes with low structural diversity, such as for example arable landscapes, than in landscapes with higher diversity (for example landscapes dominated by forest, woodland or natural pastures) (Swan & Oldham 1993).

In our study, we included land-use variables at both local (100 m buffer) and landscape (500 m buffer) scales. It is well established that different kinds of land use may have different effects depending on scale (Ficetola *et al.* 2009). For example, Jehle (2000) showed that 95% of radio-marked individuals of great crested newt stayed within 63 m from the breeding pond in an agricultural landscape in western France. On the other hand, it was found that new ponds constructed in areas with great crested newts are often colonized quite quickly if they are within approximately 500 m from an old pond (Latham & Oldham 1996, Baker & Halliday 1999, Kupfer & Kneitz 2000, Rannap 2009). Other studies showed that individuals may migrate as far as 1200 m (Kupfer 1998), which indicates that at least some individuals move over larger areas. Juvenile great crested newts may be more eager to migrate over longer distances than adults, while adults more often return to the same breeding pond and terrestrial habitat year after year (Joly & Miaud 1989, Arntzen & Wallis 1991, Kupfer & Kneitz 2000, Malmgren 2002). Swan and Oldham (1993) suggested that the great crested newt requires landscapes with a variety of land uses within 500 m of the breeding pond, but which contain areas of permanent cover (i.e. pastures, shrubs or forests) within 100 m. This study was carried out at the same scales, but could not find any clear differences between them in the land-use variables. However, abundance of old deciduous forest, fields and pastures seem to be more important at a larger scale.

To account for some local parameters related to the aquatic habitat, we included size of pond and presence of predators. Here, size of ponds did not have any relevance in predicting presence or absence of great crested newts, contrary to the results of other studies of amphibians and of species richness in general (Laan & Verboom 1990, Joly *et al.* 2001, Oertli *et al.* 2002, Knutson *et al.* 2004). However, many studies have shown that small wetlands and ponds are at least equally important as larger habitats for the diversity of amphibians and other species in a landscape (Pavignano *et al.* 1990, Oertli *et* *al*. 2002, Ficetola & De Bernardi 2004, Scheffer & van Geest 2006). In accordance with several earlier studies, presence of predators turned out to be an important negative variable (e.g. Beebee 1985, Baker & Halliday 1999, Joly *et al*. 2001, Skei *et al*. 2006). Presence of fish and crayfish is probably more or less coincidental as they are often introduced into a pond by humans or birds. Their presence is probably not primarily connected with the terrestrial environment or the surrounding landscape. Still, closeness to other aquatic habitats, especially larger lakes or rivers, greatly increases the risk of predators invading a pond, which may be particularly evident in lowland landscapes where predatory fish may more easily disperse between waterways and ponds. This is most likely one of the reasons for the negative association between abundance of lakes and rivers and presence of great crested newts, which was indicated in our study.

In conclusion, the study confirms the hypothesis that occurrence patterns of the great crested newt can be predicted by the composition of the surrounding landscape. Heterogeneous and less intensively managed areas, with a relatively large quantity of deciduous forest appear to be preferred by the great crested newt as well as by other northern European amphibians and a number of species connected to ponds and small wetlands (Møller & Rørdam 1985, Latham & Oldham 1996, Davies *et al*. 2004, Johansson *et al*. 2005, Bloechl *et al*. 2010). The value of coniferous woodland, especially old growth forest should not be overlooked, but in the management of important areas for amphibian species a higher proportion of deciduous trees should be strived for. The combination of high quality aquatic and terrestrial habitats is the key to maintaining large, viable populations. It is of vital importance to coordinate the planning of aquatic and terrestrial habitats, for example when making priorities for construction and restoration of breeding ponds for newts and other amphibians. The findings in this study may not only result in better understanding of the great crested newt, but also of species with similar requirements for habitat and landscape functioning. Conservation of the great crested newt and its habitats will benefit other amphibians and organisms that are dependent on ponds. In this perspective, and with the great crested newt being a protected species, it may serve as a useful umbrella species for the biological diversity in pondscapes (Simberloff 1998, Baker & Halliday 1999, Caro & O'Doherty 1999, Roberge & Angelstam 2004, Gustafson *et al*. 2006).

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