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Pond Quality Determinants of Occurrence Patterns of Great Crested Newts (*Triturus cristatus*)

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Abstract.—**We used principal component analysis and logistic regression to evaluate the effect of 11 pond water quality variables on the presence and absence of Great Crested Newts (*Triturus cristatus*) in a cluster of 29 ponds in south-central Sweden. Variables of importance for the patterns observed were comprised into four principal components. Using logistic regression analysis and Akaike's Information Criteria (AIC) we found that the best model explaining the distribution of Great Crested Newts included three of the principal components. Temperature and nutrient levels (nitrogen and phosphorus) were important in distinguishing between ponds with and without Great Crested Newts, whereas other physical variables were less important. Ponds with newts had higher temperatures and nutrient levels than ponds where the species was absent. Our results also suggest that the Great Crested Newt selects ponds with low nutrient levels for breeding, whereas they may be present in ponds with higher nutrient levels. Although this study was performed in a single area with a limited sample the results raise several issues of general importance for the management and conservation of Great Crested Newts in pond landscapes.**

Centuries of habitat destruction and subsequent fragmentation effects have left amphibian habitats all but nonexistent in many regions in northwestern Europe (Oldham and Swan, 1997; Houlahan et al., 2000; Alford et al., 2001; Beebee and Griffiths, 2005). For example, an estimated 95% of the total wetland area in southern Sweden was eradicated through landfilling and lowering of lakes and marshes from 1800 to about 1940 (Bernes, 1994). Ponds and tarns, and other small water bodies that constitute prime habitats for amphibians, have been regarded as useless in intensively managed landscapes, and are still overlooked in modern conservation (Hull, 1997; Angelibert et al., 2004). Although several studies have shown the importance of these habitats to local biodiversity (Friday, 1987; Linton and Goulder, 2000; Williams et al., 2003; Biggs et al., 2005), their occurrence is constantly reduced by eutrophication, introduction of fish, and by succession (e.g., Dolmen, 1982; Aronsson and Stenson, 1995; Brönmark and Hansson, 2002; Angelibert et al., 2004). Therefore, to sustain viable populations of amphibians in extensively managed landscapes, there is a need to protect, restore, and construct environments that can serve as high-quality substitute or replacement habitats (Oldham and Swan, 1997; Baker and Halliday, 1999). To achieve this, it is important to understand how abiotic and biotic factors act on the habitat requirements of species and populations to shape patterns of distribution.

The Great Crested Newt, *Triturus cristatus*, is a well-studied caudate amphibian (family Salamandridae) that is widely distributed throughout northern and central Eurasia west of the Ural Mountains (Griffiths, 1996; Thiesmeier and Kupfer, 2000; Arntzen, 2003). The species is reportedly in decline over much of its distribution, especially in Western Europe (Kuzmin, 1994; Beebee, 1997; Beebee and Griffiths, 2000; Edgar and Bird, 2006). Adult newts spend most of their life cycle in terrestrial habitats, searching for suitable food resources and daytime hiding places, and for hibernation during the winter (Beebee and Griffiths, 2000; Jehle and Arntzen, 2000; Malmgren, 2002; Malmgren et al., 2007). Terrestrial habitats are frequently a mix of grazed fields, forests, and woodland pastures, containing abundant ground cover and surface-enhancing structures such as leaf litter, dead logs, rocks, boulders, grass tussocks, and scrub (e.g., Griffiths, 1996; Latham and Oldham, 1996; Malmgren et al., 2007). Favorable sites offer a mosaic of terrestrial habitats and

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one or several aquatic habitats situated within a migration distance up to about 500–1,000 m (Jehle, 2000; Joly et al., 2001; Malmgren, 2001; Schabetsberger et al., 2004). Aquatic habitats, mainly permanent but fish-free ponds, are primarily used for breeding, egg-laying, larval development, and foraging. In Scandinavia, breeding and egg-laying take place from early April until late June (e.g., Malmgren, 2001). Female Great Crested Newts lay their eggs one by one in submerged vegetation and wrap them in leaves for protection against predators and UV-radiation (Miaud, 1994). After hatching, the larvae are aquatic predators that stay in water until metamorphosis, about three or four months later (Griffiths, 1996; Malmgren, 2002).

Breeding success and long-term survival of Great Crested Newts strongly depends on aquatic habitat quality (Beebee, 1985; Oldham et al., 2000; Malmgren, 2001). Biotic variables, such as the amount of food, presence of suitable vegetation, and presence of predators are important (Beebee and Griffiths, 2000; Joly et al., 2001; Van Buskirk, 2005; Gustafson et al., 2006). Physical, or abiotic, variables such as pond depth, surface area, pond permanence, and water temperature are also important (Langton et al., 2001; Malmgren, 2001; Van Buskirk, 2005). Therefore, variation in characteristics and the quality of aquatic habitats needs to be taken into account in the conservation and management of Great Crested Newts on the landscape level. Water quality in the broad sense is particularly important for the structural, compositional, and biological diversity of ponds and other aquatic systems (Griffiths and De Wijer, 1994). For example, acidification affects the distribution of many aquatic organisms (Griffiths, 1996; Brönmark and Hansson, 1998; Jeffries, 1998; Nicolet et al., 2004). Acidified waters prohibit many species from reproducing, or even using them as habitats, and this is also a likely scenario for the Great Crested Newt (Pierce, 1985; Griffiths and De Wijer, 1994; Skei et al., 2006). Similarly, eutrophication is a problem common to landscapes with extensive farming and high use of artificial fertilizers (Brönmark and Hansson, 1998). Oldham (1994) described overgrowth, caused by either eutrophication or discontinued grazing, or a combination of both, as the most common threat to Great Crested Newt populations. Ponds in late succession are rarely inhabited by the species (Oldham et al., 2000; Sztatecsny et al., 2004; Gustafson et al., 2006). In addition, nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+) can be toxic to amphibians at concentrations commonly found in eutrophied waters (Watt and Oldham, 1995; Ortiz et al., 2004; Smith et al., 2006; Griffis-Kyle, 2007). Thus, water quality is a strong determinant that shapes pond ecosystems and may, if not directly, at least indirectly be a key factor explaining the occurrence of Great Crested Newts and other amphibians in single ponds and in whole pond landscapes.

In this study, we test the hypothesis that pond quality characteristics act as determinants for occurrence patterns of Great Crested Newts in a well defined pond landscape. We aim to reveal factors of particular importance in determining the use of ponds as aquatic habitats by Great Crested Newts and, thereby, attempt to add to the general understanding of proper management and conservation measures. We find this of particular interest because the Great Crested Newt appears to be a good indicator (sensu Caro and O'Doherty, 1999) of pond quality for other aquatic organisms (Gustafson et al., 2006).

Materials and Methods

We examined potential breeding ponds for Great Crested Newts in the Latorp-Vintrosa area, Örebro county, south-central Sweden (approximately 59°15′N 14°56′E; Fig. 1), in the spring of 2000. The area mainly consists of small-scale mosaic agricultural landscape, resting on Cambro-Silurian sedimentary limestone bedrock. All ponds within the area ($N = 33$) were surveyed for Great Crested Newts using standard methods (see Langton et al., 2001), dividing them into ponds with newts ($N = 17$) and ponds without newts ($N = 16$). Four ponds with fish and without newts were removed from the analysis because of the strong avoidance Great Crested Newts show for ponds with presence of fish (Cooke and Frazer, 1976; Malmgren, 2001). Information on fish occurrence was based on visual observations during the survey in 2000.

Water sampling and temperature measurements were conducted in all ponds on four different occasions: when the ice began to melt (11–19 April), when reproduction began (27 April to 5 May), when reproduction ended (25–31 May), and when larvae began to hatch (26–30 June). In later analyses, mean values of the measurements on these four occasions were used. Eleven parameters of water quality were measured in each pond (Table 1). Water samples were taken 2 m from the shoreline, at a depth of 20 cm. Samples were taken at about the same time of day in all ponds. Samples were stored in cool boxes until the morning after sampling. Measurements of pH (pH-indicator pH M80), alkalinity (ALK; alkalinity test kit with digital titration Hach AL-DT), and electrical conductivity (COND; Hach conductivity/TDS meter) were carried out in the laboratory

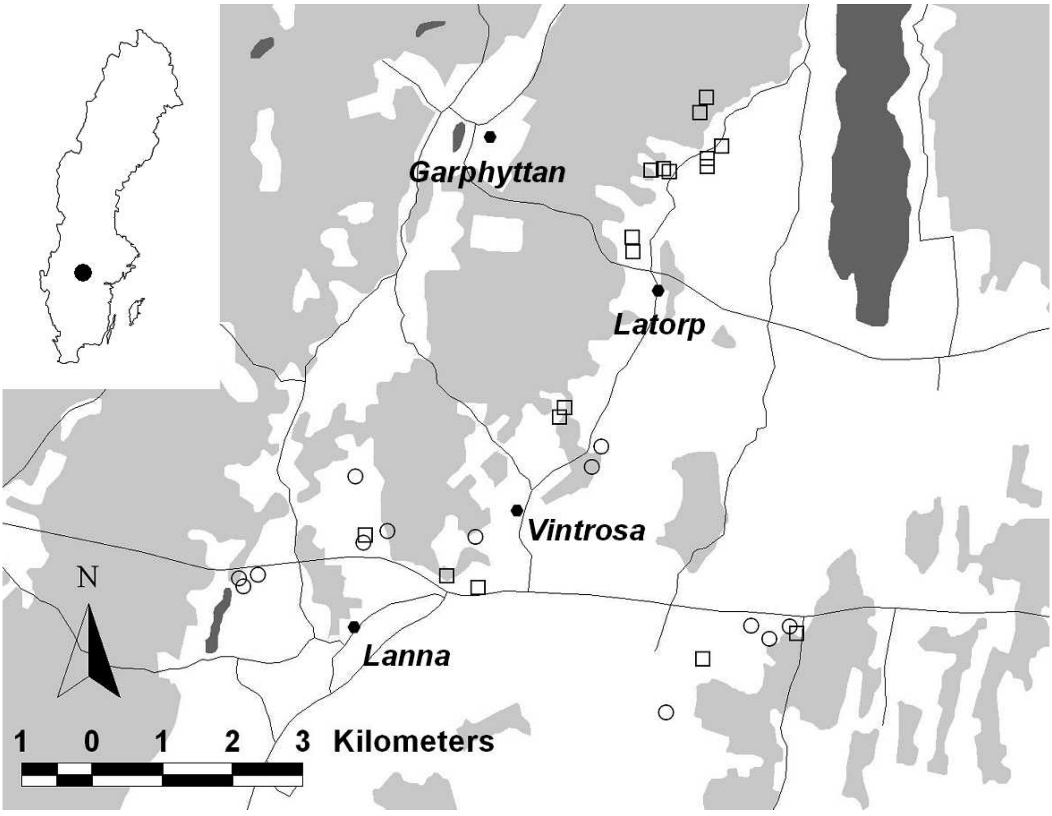

FIG. 1. Location of ponds with presence (open circles) and absence (open squares) of Great Crested Newts in the landscape west of Örebro. Light gray shading represents forests and dark gray shading stand for larger water bodies. Black lines represent roads. The map in the left upper corner shows the general location of study area in Sweden.

the morning after the sample was taken. Other variables were measured after deep freezing of samples—hardness (dH; titration with Merck, Reagent Kit); color (COL; spectrophotometer Hach DR/2000); nitrate and nitrite (N/N; Tectator Aquatec, 5400 Analyser, 5027 Sampler); ammonia (AMM; Tectator Aquatec 5400, Analyser, 5027 Sampler); total nitrogen (NTOT; Tectator Aquatec, 5400 Analyser, 5027 Sampler); phosphate-phosphorus (PO_4; Flow Injection Analysis Tectator, 5012 Analyzer, 5042 Detector, 5027 Sampler); and total phosphorus (PTOT; Tectator Aquatec, 5400 Analyser, 5027 Sampler). Temperature (TEMP) was measured in the field 2 m from the shore, at a depth of 30 cm.

Initially the two groups of ponds (with newts and without newts) were compared using two-sample *t*-tests, for each of the eleven 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 four principal components were selected for further analyses, based on eigenvalues (>0.7) and the shape of scree-plots (Everitt and Dunn, 2001). We interpreted the association between the four 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 logistic regression with a backward successive exclusion of variables. Model significance was checked with likelihood ratio tests (Hosmer and Lemeshow, 2000). Models were compared and ranked using Akaike's Information Criterion (AIC; Burnham and 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 impor-

TABLE 1. Group means, standard error and range for pond quality variables on a sample of 29 ponds from south-central Sweden where Great Crested Newts (*Triturus cristatus*) was either present or absent. Univariate comparisons of the two pond groups with *t*-tests for independent samples. Significant results in bold. The first six variables are considered as physical variables in the text and the last five are considered as chemical variables.

Variable (N = 12)	With newts (N = 17)	Without newts (N = 12)		
Description (abbr.)	Mean ± SE	Mean ± SE		
Measurement unit	Min–Max	Min–Max	*t*-value	*P*
Acidity (pH)	6.73 ± 0.16	6.79 ± 0.18		
pH	5.21–7.99	5.41–7.25	−0.28	0.776
Alkalinity (ALK)	1.98 ± 0.28	3.01 ± 0.51		
$mekv \cdot l^{-1}$	0.15–4.32	0.29–5.55	−1.32	0.195
Hardness (dH)	7.83 ± 0.76	10.70 ± 1.57		
$d\ ^\circ$	3.00–14.75	2.00–18.00	−1.02	0.315
Conductivity (COND)	0.27 ± 0.03	0.35 ± 0.05		
$mS \cdot cm^{-1}$	0.08–0.52	0.07–0.62	−1.09	0.285
Color (COL)	67.50 ± 18.25	60.82 ± 14.93		
$mg\ Pt \cdot l^{-1}$	14.00–344.00	14.75–209.50	0.16	0.873
Temperature (TEMP)	11.79 ± 0.31	10.40 ± 0.30		
°C	9.38–13.75	8.63–11.75	3.10	**0.004**
Total nitrogen (NTOT)	1007.01 ± 126.22	676.70 ± 128.74		
$\mu g \cdot l^{-1}$	200.10–1914.54	263.27–1911.68	1.66	0.109
Nitrate + nitrite (N/N)	542.25 ± 194.85	337.70 ± 169.40		
$\mu g \cdot l^{-1}$	10.00–2324.25	10.00–1912.13	0.10	0.922
Ammonia (AMM)	109.56 ± 32.91	75.17 ± 18.43		
$\mu g \cdot l^{-1}$	25.00–512.87	25.00–217.21	0.23	0.818
Total phosphorus (PTOT)	121.34 ± 39.99	42.25 ± 10.09		
$\mu g \cdot l^{-1}$	12.59–707.77	10.00–109.62	2.24	**0.034**
Phosphate-phosphorus (PO_4)	33.20 ± 6.33	18.26 ± 0.55		
$\mu g \cdot l^{-1}$	16.54–121.00	15.94–21.99	2.49	**0.019**

tance of the different models ($AIC_{ci} - AIC_{cmin} = \Delta_i$). All models with $\Delta_i < 2$ can be considered equal in making inferences (Burnham and Anderson, 2002). We also calculated Akaike weights (w_i), to determine the strength of evidence for each model (Burnham and Anderson, 2002).

After testing for differences between the two groups of ponds with or without Great Crested Newts, the ponds with newts were divided into ponds with or without reproduction of Great Crested Newts. A pond was considered to have reproduction if newt larvae were found in the pond during surveys in 1999 or 2000. This resulted in three new groups of ponds: without newts (N = 12), with newts and without reproduction (N = 12), and with reproduction (N = 5). To test for differences among the three groups, we used multinomial logistic regression, for each of the four principal components.

RESULTS

For three of the measured variables there were significant differences between ponds with and without Great Crested Newts (Table 1). Temperatures were higher in ponds in which the species occurred (t = 3.10, P = 0.004, df = 27). Further, both total phosphorus (t = 2.24, P = 0.034, df = 27) and the phosphate/phosphorus ratio (t = 2.49, P = 0.019, df = 27) were higher in ponds with presence of Great Crested Newts.

The principal component analysis resulted in four components with an eigenvalue exceeding 0.7 (Table 2). Together the four components explained more than 85.5% of the variance. The first component explained 36.7% of the variance and was significantly associated with variables representing chemico-physical attributes (pH, ALK, dH, and COND). The second component explained 24.1% of the variation and was positively associated with total amount of nitrogen (NTOT) and the phosphate to phosphorus ratio (PO_4) and had high levels for nutrients in general (i.e., the levels of organic compounds; NTOT, N/N, AMM, PTOT, and PO_4). The third component was positively associated with temperature (TEMP) and total phosphorus (PTOT) and explained 17.6% of the variation. The fourth component, which explained another 7.1% of the variation, was significantly associated with the levels of nitrate and nitrite (N/N).

The results from the backward logistic regression procedure are presented in Table 3.

TABLE 2. Multivariate loadings of water quality variables from principal component analysis for components 1, 2, 3 and 4. Bold values depict significant associations with the axes. The table also shows eigenvalue, variance (%), and cumulated variance (%) for the four components.

Variable	PC 1	PC 2	PC 3	PC 4
pH	**0.845**	0.023	0.327	0.107
ALK	**0.964**	−0.063	0.087	−0.082
dH	**0.949**	0.079	0.135	−0.181
COND	**0.932**	0.115	−0.067	−0.063
COL	−0.686	0.218	0.257	−0.454
TEMP	−0.063	−0.087	**0.771**	0.497
NTOT	−0.190	**0.868**	−0.073	0.135
N/N	0.088	0.508	−0.681	**0.442**
AMM	0.316	0.641	−0.410	−0.223
PTOT	0.009	0.681	**0.649**	−0.096
PO_4	−0.105	**0.825**	0.286	0.028
Eigenvalue	4.041	2.646	1.938	0.782
Variance (%)	36.736	24.055	17.620	7.108
Cumulated (%)	36.736	60.791	78.411	85.519

The division of the investigated ponds into two a priori groups (i.e., with and without newts) was significantly ($P < 0.05$) explained by three different combinations of the first four PCA-axes and with principal component four (PC 4) alone. The best model according to Akaike's test was the second step, containing PC 2, PC 3, and PC 4. This model had the lowest AIC_c and Δ_i and the highest Akaike weight (w_i). The principal components in the model corresponded to high values in nitrogen (N/N, AMM, and NTOT), phosphorus (PO_4 and PTOT), and temperature.

When comparing ponds without newts, ponds with newts but without reproduction, and ponds with reproduction of Great Crested Newts, the only significant difference among the groups was found on PC 2 (Model $P <$ 0.001), which was highly correlated with variables corresponding to nutrients (Table 4). The group with Great Crested Newts but without reproduction had significantly higher values than ponds without newts ($B = 2.476$, $P = 0.010$) and ponds with reproduction ($B = 5.400$, $P =$ 0.007). There was no difference between ponds without newts and ponds with reproduction.

DISCUSSION

Our results showed that there were systematic differences in water quality between ponds with and without Great Crested Newts. The distinction could best be explained by combined differences in levels of nitrogen, phosphorous, and temperature. These parameters generally had higher values in ponds with newts compared to ponds without newts. Physical parameters appeared subordinate in distinguishing between the two groups of ponds. The same

TABLE 3. Results from logistic regression analysis with backward stepwise exclusion of variables (SPSS, 14.0). Four variables that are the four first components from the principal component analysis in Table 2 were included in the initial step. Models are compared using Δ_i and Akaike weights (w_i). Significant values in bold.

Model	B	SE	Wald's statistic	P				
Step 1								
Constant	0.916	0.632	2.103	0.147	Nagelkerke R square	0.600	Δ_i	1.158
PC 1	−0.719	0.574	1.571	0.210	Hosmer-Lemeshow test	0.494	w_i	0.312
PC 2	1.305	0.682	3.662	0.056	Model P	0.002		
PC 3	1.658	0.820	4.084	**0.043**	−2log(likelihood)	22.26		
PC 4	1.641	0.734	4.998	**0.025**	AICc	34.86		
Step 2								
Constant	0.792	0.574	1.907	0.167	Nagelkerke R square	0.552	Δ_i	0
PC 2	1.251	0.648	3.727	0.054	Hosmer-Lemeshow test	0.929	w_i	0.557
PC 3	1.726	0.906	3.631	0.057	Model P	0.002		
PC 4	1.513	0.698	4.702	**0.030**	−2log(likelihood)	24.04		
					AICc	33.71		
Step 3								
Constant	0.514	0.462	1.240	0.266	Nagelkerke R square	0.353	Δ_i	3.771
PC 2	0.888	0.512	3.009	0.083	Hosmer-Lemeshow test	0.275	w_i	0.085
PC 4	1.045	0.498	4.402	**0.036**	Model P	0.012		
					−2log(likelihood)	30.52		
					AICc	37.48		
Step 4								
Constant	0.421	0.418	1.012	0.314	Nagelkerke R square	0.217	Δ_i	4.996
PC 4	0.964	0.473	4.151	**0.042**	Hosmer-Lemeshow test	0.478	w_i	0.046
					Model P	0.024		
					−2log(likelihood)	34.24		
					AICc	38.70		

TABLE 4. Results from multinomial logistic regression analysis (SPSS, 16.0). The difference between three categories of ponds (ponds without newts, ponds with newts but no reproduction, and ponds with reproduction of newts) was tested, using the four first components from the principal component analysis in Table 2. Models are compared using Δ_i and Akaike weights (w_i). Significant values in bold.

Model	B	SE	Wald's statistic	P				
PC 1								
Reference category = 0					Nagelkerke R square	0.112	Δ_i	20.57
1	−0.218	0.454	0.230	0.804	Model P	0.224	w_i	<0.0001
2	−0.936	0.577	2.637	0.104	−2log(likelihood)	56.95		
					AICc	65.41		
Reference category = 2								
0	0.936	0.577	2.637	0.104				
1	0.719	0.551	1.703	0.192				
PC 2								
Reference category = 0					Nagelkerke R square	0.637	Δ_i	0
1	2.476	0.967	6.554	**0.010**	Model P	**0.001**	w_i	0.9998
2	−2.925	1.741	2.822	0.093	−2log(likelihood)	36.38		
					AICc	44.84		
Reference category = 2								
0	2.925	1.741	2.822	0.093				
1	5.400	2.001	7.281	**0.007**				
PC 3								
Reference category = 0					Nagelkerke R square	0.146	Δ_i	19.59
1	0.773	0.498	2.405	0.121	Model P	0.138	w_i	<0.0001
2	1.000	0.638	2.450	0.118	−2log(likelihood)	55.97		
					AICc	64.43		
Reference category = 2								
0	−0.999	0.638	2.450	0.118				
1	−0.226	0.575	0.155	0.694				
PC 4								
Reference category = 0					Nagelkerke R square	0.189	Δ_i	18.32
1	0.904	0.498	3.297	0.069	Model P	0.073	w_i	0.0001
2	1.123	0.647	3.009	0.083	−2log(likelihood)	54.70		
					AICc	63.16		
Reference category = 2								
0	−1.123	0.647	3.009	0.083				
1	−0.219	0.593	0.136	0.712				

applied to the differences between ponds with or without reproduction of Great Crested Newts.

High water temperature in ponds is in most cases a secondary effect of high insolation; ponds that are more exposed to the sun have higher temperatures and, as a consequence, higher productivity (e.g., Werner and Glennemeier, 1999; Oldham et al., 2000; Thiesmeier and Kupfer, 2000). Thus, warmer ponds are likely to have higher diversity, and pond temperature may indicate species-rich habitats, especially if such ponds are also rich in nutrients. Gustafson et al. (2006) demonstrated that the Great Crested Newt is a useful indicator of high macrophyte diversity in ponds. This could be because this species selects productive ponds with higher than average temperatures. Such habitats are likely to be the most favorable, because they allow for higher growth rates and better survivorship among eggs and larvae (see Skelly et al., 1999; Werner and Glennemeier, 1999). In our study area located along the northern edge of the distribution of Great Crested Newts, water temperature might also be a limiting factor for reproductive success and, therefore, even more important. The length of the breeding season depends on the amount of insolation of the aquatic habitat, with rapid warming and early break up of ice in spring and subsequently shorter egg and larval development (Griffiths and De Wijer, 1994; Griffiths, 1996; D'Amen et al., 2007).

According to our results, Great Crested Newts are more likely to occur in ponds with higher nutrient content. High levels of different types of nitrogen (N) and phosphorus (P) in the water signify high nutrient availability, which is the basis for high productivity. P is usually a limiting resource for primary production and growth in aquatic systems, but when P is abundant, N often replaces it as a limiting resource (Brönmark and Hansson, 1998). Great Crested Newts most likely prefer and thrive in ponds with a diversity and richness of food resources, such as aquatic invertebrates and eggs and larvae of other amphibians (Thurnheer and Reyer, 2001). The species is also dependent on rich and varied vegetation for egg laying and protection from predators (Miaud, 1993; Gustafson, 2006). In ponds with high productivity, these resources are often abundant. However, ponds too rich with nutrients are frequently subjects of eutrophication, with domination of certain plant species, low levels of oxygen, and generally poorer water quality and substantial overgrowth (Engelhardt and Ritchie, 2001, 2002; Loreau et al., 2001; Knutson et al., 2004). Thus, high amounts of available nutrients could signify favorable conditions for productivity but also an enhanced risk for early pond ageing (i.e., speeding succession). Our results clearly indicate that ponds with reproduction of Great Crested Newts have lower available levels of nitrogen and phosphorus than ponds where the species is present but not reproducing, suggesting a nonlinear convex relationship. Thus, the species appear to prefer a stage in pond succession where productivity is high and the amounts of available nutrients are at moderate levels, which is consistent with patterns previously observed by Gustafson et al. (2006). Later succession stages, where ponds are overgrown because of eutrophication, or where nutrients are not consumed because of low insolation caused by shading from surrounding trees, appear abandoned by newts.

From an ecosystem perspective, ponds with optimal productivity will have low or almost nonexistent levels of free nutrients (because they are incorporated in biomasses that compete for their use) but high biodiversity. Ponds with high levels of available nutrients may be suitable for foraging by adult newts, but the quality may be too poor for reproduction or prohibits survival of eggs and larvae. Studies have confirmed that high levels of available P and N negatively affect the presence of Great Crested Newts (Karlström, 1995; Karlström and Sjögren-Gulve, 1997). Further, other amphibians are negatively affected by high concentrations of ammonium nitrate (Watt and Jarvis, 1997; Ortiz et al., 2004). For example, high contents of ammonium nitrate retard larval development in Smooth Newts (*Triturus vulgaris*), making larvae grow more slowly (Watt and Oldham, 1995). Ammonium is toxic for amphibians at levels from 5–25 mg/l at pH 8, depending on temperature (Diamond et al., 1993; Berg, 1996). In our study the highest measured value for ammonium was 0.5 mg/l, in a pond with Great Crested Newts but no reproduction. However, toxicity of ammonium can depend on temperature and is higher with higher pH (Berg, 1996). This could be a problem in the study area, because the soils and bedrock are calcium rich and the pH of the ponds generally is at or even above neutral (pH 7). Negative effects of these compounds in the field are not clear, and harmful levels are possibly only reached in extreme agricultural landscapes (Laposata and Dunson, 2000; Johansson et al., 2001; Ortiz et al., 2004). Because of the low-level agricultural use of the investigated landscape, extremely high levels of N and P are unlikely. Instead these compounds may be limiting factors, which can explain the results of our study.

Great Crested Newts are found in both acidic and alkaline ponds but tend to be found more often in waters that are close to neutral or slightly alkaline (Cooke and Frazer, 1976; Denton, 1991; Karlström and Sjögren-Gulve, 1997; Skei et al., 2006). Several studies have shown increased embryonic death, reduced hatchability, and sublethal responses of amphibians at low pH (Clark and LaZerte, 1985; Freda and Dunson, 1985; Andrén et al., 1988; D'Amen et al., 2007). This also applies to *T. cristatus* (Griffiths and De Wijer, 1994). However, Beebee (1996) noted that interactions among water chemistry parameters complicate the interpretation of pH tolerance in amphibians based solely on field studies. The lowest pH-value in our study was 5.2, in a pond with reproduction of Great Crested Newts. However, there was no significant difference in pH between the two groups of ponds in this study, and pH together with other chemo-physical parameters on PC 1 did not appear important in the discrimination between the two groups of ponds in our study. Skei et al. (2006) found a nonlinear convex relationship between pH and probability of occurrence of Great Crested Newts in central Norway.

In western France, Sztatecsny et al. (2004) found that the best models explaining abundance of embryos and larvae of Great Crested Newts contained the variables floating vegetation (highest embryo abundance in intermediate ponds), pond size (negative for embryo abundance), shade (negative for larval abundance), and the interaction between phosphate and nitrate (positive for larval abundance). The results of the present study are consistent with their findings regarding the importance of insolation (high water temperature) and actual levels of nitrate and phosphate.

Several efforts have been made to identify determinants of distribution patterns for newts and other amphibians. Complex interactions between water quality and biotic factors, such as food and shelter availability, predation and competition, appear to be the key-factors affecting the distribution of amphibians (Griffiths et al., 1993). Our study focused exclusively on water quality and confirms the complexity of how environmental factors affect the occurrence of Great Crested Newts. Most studies investigating habitat characteristics of ponds and their surroundings have shown that physical, biological and landscape characteristics appear more important than chemical characteristics for biodiversity of these aquatic environments (e.g., Laan and Verboom, 1990; Pavignano et al., 1990; Sztatecsny et al. 2004; Denoël and Ficetola, 2007). This may be explained by the fact that many organisms are dependent on both aquatic and terrestrial environments during different stages of their lifecycles, and therefore, juxtaposition of these two environments is important. Moreover, landscape composition, topography and hydrology may directly affect the quality of aquatic environments (Brönmark and Hansson, 1998; Jeffries, 2005; Johansson et al., 2005).

The ponds used in this study are situated in an area with fairly homogenous and almost ideal conditions for the Great Crested Newt (i.e., with many ponds and a mosaic of pastures and hardwood forest in an agricultural landscape, on calcium-rich bedrock). Therefore, the data presented here are likely to represent only a narrow range of conditions used by this species. A more inclusive approach, where more of the various habitat types that the species use are represented, would require a large set of ponds located in different landscape types. Although such an approach would present the opportunity for better and more exact predictions, we conclude that the analysis presented here demonstrates that the Great Crested Newt is an amphibian with well-defined and predictable aquatic habitat requirements. Further, we believe it is no coincidence that the majority of ponds where newts are found in our study lack evidence of breeding success. In the study area, the rate of pond loss is much higher than the rate at which new breeding ponds are added (which is next to nothing; JCM, unpubl. data). Therefore, most of the ponds are likely to be in late succession, either as an effect of discontinued grazing in or around the water bodies, eutrophication, or from shading caused by scrub or forest growing up around the ponds edge (see e.g., Ihse, 1995; Johansson et al., 2005). If there is an optimum stage at which Great Crested Newts thrive the best, their long-term survival on the landscape scale depends on the rate at which new ponds are added (e.g., through construction), or at which old ponds are restored, together with proper maintenance. The results also clearly show that Great Crested Newts use ponds differently in relation to habitat quality; some ponds are not used at all, others are in effect only used as ''resting sites'' (i.e., sinks), whereas only a small proportion of the ponds are useful as good ''nesting sites'' (i.e., sources). Indeed, this suggests that reproductive success of Great Crested Newts may be a very useful indicator of warm and highly productive species rich aquatic habitats without fish. This emphasizes the possible importance of the Great Crested Newt as a reliable indicator species (cfr., Gustafson et al., 2006).

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