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GEOGRAPHIC VARIATION IN HABITAT REQUIREMENTS OF TWO COEXISTING NEWT SPECIES IN EUROPE

RANNAP, R., LÕHMUS, A. and LINNAMÄGI, M.

Institute of Ecology and Earth Sciences, University of Tartu
Vanemuise 46, 51014 Tartu, Estonia; E-mail: riinu.rannap@ut.ee

Habitat requirements of widely distributed species often vary geographically, and local habitat studies may not be relevant for populations elsewhere. This is particularly important for conservation planning of threatened species. In this study, we explored two wide-ranging coexisting newt species that have contrasting conservation status in Europe: the northern crested newt (*Triturus cristatus*) and the smooth newt (*T. vulgaris*). The aim was to identify geographic patterns in their essential habitat characteristics, which might explain also the contrasting status of these species. First, in the northern part of their range (in Estonia), a comparative case study was carried out following the methodology of an earlier study conducted in Denmark. The majority of habitat preferences overlapped in those two countries: in the northern crested newt, influential habitat characteristics were related to the terrestrial habitat, while they were linked to the aquatic habitat in the smooth newt. However, a literature review demonstrated that the habitat characteristics of those newts vary over broader scales. For the northern crested newt, sun-exposed water bodies were essential at high latitudes, while land cover type (woodland/scrub) appeared important for the smooth newt in peripheral populations only. We suggest that the contrasting status of two species is related to their different habitat requirements.

Key words: amphibians, distribution range, habitat characteristics, *Triturus cristatus*, *T. vulgaris*

INTRODUCTION

Wide-ranging species may exhibit substantial geographic variation in habitat requirements (COLLINS 1983, CONSTIBLE *et al*. 2009). Habitat components critical for a species in one part of its range may be less important or even avoided in another area (PARODY & PARKER 2002, VÄLI *et al*. 2004). Therefore, habitat information is required from different parts of the range, particularly for threatened species, for which proper identification of critical habitat conditions forms a basis for effective management (GRAZYBOWSKI *et al*. 1994, WHITTINGHAM *et al*. 2006).

The northern crested newt (*Triturus cristatus* LAURENTI, 1768) is a widely distributed European amphibian, which is in decline in most countries of its range (BEEBEE 1997, EDGAR & BIRD 2006) and is listed in the Annex II and IV of the EU Habitats Directive (92/43/EEC). Such status requires habitat protection and, as a pre-requisite, explicit understanding of its habitat requirements throughout the European Union. Although habitats of the northern crested newt have been described in many range countries, its requirements have often remained obscure because of small sample sizes (BEEBEE 1985, STUMPEL 2004, DENOËL & FICETOLA 2007, 2008), and the geographic variation in those requirements has not been examined.

Over most of its range the northern crested newt is sympatric with the smooth newt (*Triturus vulgaris* LINNAEUS, 1758); these species can often be found in the same landscapes and water bodies (ZUIDERWIJK 1986, DOLMEN 1988, GRIFFITHS & MYLOTTE 1987, VAN BUSKIRK 2007). In contrast to the mostly declining status of the northern crested newt, the smooth newt is locally abundant (e.g. GRIFFITHS & MYLOTTE 1987, DOLMEN 1988, DENOËL & FICETOLA 2008). The proposed factors for the declines of the crested newt are habitat-related: loss of ponds, habitat fragmentation, introduction of fish, changes in agricultural systems (BEEBEE 1997, JOLY *et al*. 2001, GUSTAFSON *et al*. 2009). Yet, those processes have not affected the coexisting smooth newt to such an extent, which might be related to distinct (micro)habitat requirements. To explore such potentially different key factors, habitat requirements of those newts should be compared in areas of their frequent coexistence across the range.

Our study explores habitat features of the northern crested newt and the smooth newt over a latitudinal gradient from 44°N to 64°. First, we present a comparative case study in the northern part of the range, in Estonia, where the crested newt has declined substantially during the second half of 20th century, while the smooth newt has remained abundant. The study design (e.g. selection of water bodies, set of variables, field methods used) and analyses follow those previously used ca. 1000 km away, in Denmark (RANNAP *et al*. 2009) thus allowing a direct comparison with the latter. Secondly, we review published studies for a wider, but more general, perspective on the consistency of habitat requirements of these wide ranging species over latitudinal gradient and in respect to range edge. We assume, for example, that sun-exposed breeding sites as well as high-quality terrestrial habitats may be particularly preferred at high latitudes. Finally, we synthesize the findings of the case study and the review to distinguish key factors that could explain the contrasting conservation status of those species.

MATERIAL AND METHODS

Determining habitat requirements in Estonia

The fieldwork was carried out by 12 herpetologists in June 2007 in two areas in southern Estonia, hemiboreal Europe: Haanja (16 900 ha; 27°2’E; 57°43’N) and Otepää (22 430 ha; 26°25’E; 58°5’N) Landscape Protected Areas. The hilly moraine landscape of the Haanja area represents a mosaic of forests (45%), grasslands (21%) and small extensively used fields and farmlands. The Otepää area (42% forest) also has a varied hilly relief, but the farming practices are more intense than in Haanja. A total of 325 small water bodies (3–250 m^2 in size; hereafter: ponds) were studied: 135 in Haanja and

190 in Otepää. Of those, 139 ponds had been restored or created for the northern crested newt or the common spadefoot toad (*Pelobates fuscus* LAURENTI 1768) in 2005–2006, the rest included both temporary and permanent natural water bodies (beaver ponds, natural depressions, small lakes) as well as man-made ponds (e.g. sauna, garden and cattle ponds).

For each water body, eight aquatic and four terrestrial characteristics were assessed (Table 1); four of those were measured from the Estonian base map using MapInfo Professional 8.5 software. Land cover within a 50 m radius around the water body was classified as one of the four main biotopes (forest; cultivated field; grassland; farmyard/houses) or their combination. Such area comprises a typical home range for adult northern crested newt (JEHLE 2000, MÜLLNER 2001). In addition, distance of the pond to the nearest pond known to be inhabited by the northern crested newt (based on consolidated monitoring, 2001–2007) and to the nearest forest edge were measured.

Presence of the newt species was assessed by searching for their eggs and standard dip-netting of larvae (SKEI *et al*. 2006) covering all important microhabitats for newts. Each pond was studied for maximum 15 minutes during one visit in June 2007 by two herpetologists (one searching for eggs; another dip-netting for larvae). Hence, due to the single visit to each pond, random effects in the number of caught individuals were probably large and we used only presence-absence for analyses. By focusing on eggs and larvae (i.e. breeding attempts) the ‘presences’ probably do not contain many marginal habitats. We established the presence of fish, using combined data of visual observation, dip-netting, and information from local people.

The analysis followed the procedure used in Denmark (RANNAP *et al*. 2009). First, χ^2 tests were conducted to check whether the presence of fish constituted a limiting factor for the presence of newts (JOLY *et al*. 2001, SKEI *et al*. 2006, RANNAP *et al*. 2009). Once this key factor was established (see Results), water bodies populated by fish were omitted from further analysis. For the other factors, multiple logistic regression models were elaborated based on the remaining 240 ponds (114 in Haanja, 126 in Otepää) and according to the procedure proposed by HOSMER and LEMESHOW (1989): (1) univariate analyses were performed for each of the 12 independent variables; (2) preliminary multivariate models were built including all the potentially important variables according to the univariate analyses, (3) non-significant and/or redundant variables were omitted considering their biological meaning and instability in different models. In the steps (1) and (2), the significance level (estimated by likelihood-ratio tests) was set at $\alpha < 0.15$ (to retain variables that could gain significance in combination with other variables); in the step (3), $\alpha < 0.05$ was used. Performance of the final multivariate models was assessed by comparing observed versus expected presence/absence using the breakpoint at 0.5 for the expected values.

Literature review

In total, 35 published habitat studies over the range of those species were found and assessed (Fig.1, Appendix 1). Twenty-nine studies compared inhabited and uninhabited water bodies; six concluded habitat preferences based only on a single pond or several ponds. The studies had been conducted in 13 countries over a latitudinal gradient from 44°N to 64° (Fig. 1). Sixteen studies explored both species, while nine papers only focused on the northern crested newt and nine on the smooth newt. The number of examined water bodies ranged from one to 371 (median 82), with 3–33 (median 11) habitat characteristics reported. In 27 studies both aquatic and terrestrial habitats were examined, the rest focused on either aquatic or terrestrial habitat.

For each species, we arranged the reported habitat relationships latitudinally and with respect to range centre to detect geographic patterns. Despite of many habitat features studied, the set of characteristics that could be compared was much reduced because of a limited overlap among studies.

Table 1. Variables measured in the aquatic and terrestrial habitat of the northern crested newt (T.cri. = *T. cristatus*) and the smooth newt (T.vul. = *T. vulgaris*) in Estonia[a]

Acronym	Description of the variable	N	p	
			T.cri.	T.vul.
Type	Type of the water body (6 types)	240	0.092	0.004
Depth	Maximum depth of the water body (m)	200	0.311	0.020
Management	Unmanaged vs. restored/new-dug pond	240	0.003	0.002
Slope	Mean slope (°) of the four cardinal banks of the pond	217	0.191	<0.001
Sediment	Type of pond bottom (4 types: clay, sand, mud, peat)	228	0.072	0.694
Water	Transparency or colour of the water (4 types: clear, brown, muddy, algae-green)	228	0.045	0.047
Shade	% of the water table of the pond under shadow	219	0.020	0.975
Vegetation	% of pond area covered by water vegetation	233	0.889	0.640
Land cover < 50 m*	Main land-cover within 50 m (6 types: grassland with and without forest, field with and without forest, field/grassland mosaic with and without forest)	240	0.005	0.823
Farm < 50 m*	Presence of farms/buildings within 50 m around the pond	240	0.80	0.01
Nearest forest*	Distance from the pond to the nearest forest edge (m)	240	0.002	0.655
Nearest T.cri. pond*	Distance to the nearest pond with *Triturus cristatus* (m)	240	<0.001	-
Fish	Presence of fish in the pond	325	<0.001	0.02

[a]Variables marked with the asterisk (*) were measured from the digital base map of Estonia.

Most of the habitat characteristics (N = 24) were recorded fewer than in five papers (Appendix 1) and also the rest were often reported in different units not allowing the use of means and deviations for meta-analyses. Given also the diversity of uni- and multivariate analysis conducted in different studies, we only could make a general assessment of the likely patterns across these datasets.

RESULTS

The case study in Estonia

The smooth newt was present in 159 ponds (49 %) and the northern crested newt in 110 ponds (34 %) of the 325 inventoried, with 66 ponds being inhabited by

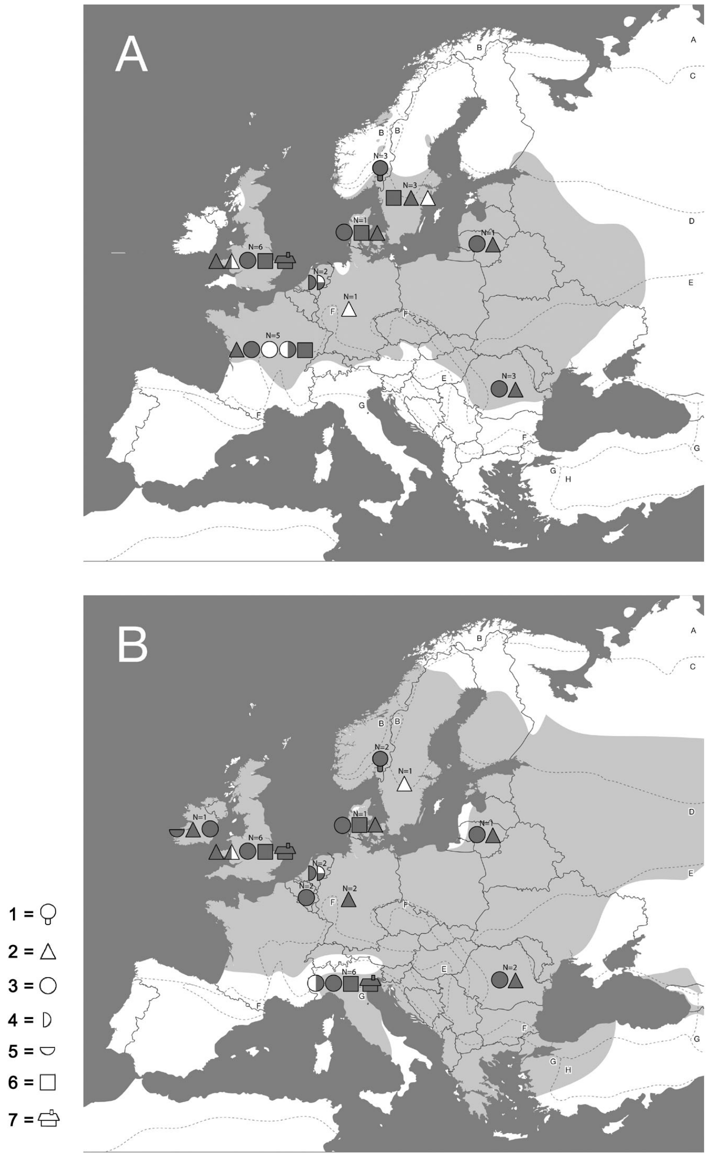

Fig. 1. (A) Distribution of the northern crested newt (*Triturus cristatus*) and (B) the smooth newt (*T. vulgaris*) in Europe (ARNOLD 2002), and their habitat studies performed by country. The symbols indicate (i) landscape types where study was conducted (1 = woodland mosaic with bogs; 2 = woodland mosaic with semi-natural areas; 3 = woodland mosaic with agricultural areas; 4 = inland dunes; 5 = bogs; 6 = agricultural areas; 7 = urban areas) and (ii) the inclusion of terrestrial and aquatic habitat features (filled symbols – both examined; half filled – aquatic habitat only; hollow symbol – terrestrial habitat only). Vegetation zones (according to AASMÄE 2005): A, tundra ; B, alpine tundra; C, taiga; D, temperate forest; E, temperate steppe; F, mountain forest; G, Mediterranean forest; H, dry steppe

Table 2. Results of logistic regression models of habitat factors explaining the presence of the northern crested newt (*Triturus cristatus*) and the smooth newt (*T. vulgaris*) in 240 ponds in Estonia.

Variable	*Estimate*	*SE*	*LL*	χ^2	*p*
The northern crested newt *Triturus cristatus* (model log-likelihood –110.5, $p < 0.0001$)					
Nearest forest	–0.01	0.004	–113.6	6.2	0.013
Nearest T.cri. pond	–0.002	0.0005	–154.9	88.8	< 0.001
The smooth newt *Triturus vulgaris* (model log-likelihood –129.1, $p < 0.013$)					
Max depth	0.85	0.42	–131.5	4.6	< 0.032
Water			–133.2	8.2	0.045
algae-green	–0.73	0.53			
brown	–0.006	0.32			
clear	0.67	0.26			

LL – log-likelihood of the variable.

both species. Fish were present in 85 ponds, mostly (86%) crucian carp (*Carassius auratus gibelio* BLOCH, 1782), an alien species in Estonia; but also nine-spined stickleback (*Pungitus pungitus* LINNAEUS, 1758) in 7% of ponds; tench (*Tinca tinca* LINNAEUS, 1758) in 5%; and pike (*Esox lucius* LINNAEUS, 1758) in 2% of ponds. Sixteen (19 %) ponds with fish also hosted the northern crested newt (eggs or adults only) and 33 (39 %) hosted the smooth newt (including three ponds with larvae). Hence, both species avoided water bodies with fish (χ^2-tests: χ^2_1 =12.0, $p < 0.001$ for the crested newt; $\chi^2 = 5.1$, $p = 0.020$ for the smooth newt) thus omitted from further analysis.

Among the 240 water bodies without fish, the northern crested newt presence was explained by shorter distances to the nearest forest edge and to the nearest pond occupied by conspecifics (Table 2). The logistic model incorporating those variables correctly classified 78% of observations (84% presences, 74% absences). Four additional factors, which strongly co-varied with the two extracted (Table 3), appeared significant at the univariate stage of the analysis only ($p = 0.05$; Table 1): (1) land cover within 50 m around ponds (grassland-forest mosaic most favoured, followed by field-grassland-forest mosaic and plain grassland; cultivated fields avoided); (2) shade (negative); (3) water transparency or colour – clear or brownish water preferred, muddy and algae-green avoided; (4) pond management (restored or newly dug ponds preferred).

The smooth newt presence was also explained by two characteristics (Table 2): maximum depth of the pond (positive) and water transparency or colour (clear preferred, algae-green avoided). The two-factor model classified 61 % of observations correctly (69 % presences, 51 % absences). Again, four additional factors appeared significant in the univariate stage of the analysis (Table 1): (1) the type of

Table 3. Redundancy of the ecological variables, which attained p ≤ 0.15 for either species in univariate analyses of Estonian study. See Table 1 for acronyms and sample sizes.

Variable	Related variables[a]
Type	Shading***, Slope***
Depth	Slope***, Management*
Shading	Type***, Management***, Sediment***, Land cover < 50 m ***, Nearest forest ***, Nearest *T. cristatus* pond***
Management	Shading***, Slope***, Depth*
Slope	Type***, Depth***, Management***, Farm < 50 m**
Sediment	Shading***
Land cover < 50 m*	Shading***, Near. forest ***
Farm < 50 m*	Slope**
Nearest forest*	Shading***, Land cover < 50 m***, Management*
Nearest *T. cristatus* pond*	Shading***, Management***

[a]significance according to Spearman correlation (continuous variables), chi-square test (categorical variables) or Kruskal-Wallis ANOVA (combination of the two): * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

water body (man-made ponds preferred, natural water bodies avoided); (2) slope of the banks (positive); (3) presence of farmyard/houses within 50 m (positive); and (4) pond management (negative). Although it was possible to construct alternative multivariate models with those factors, their classification success was clearly worse than of the selected model.

Geographic variation in habitat requirements

The smooth newt was more common and abundant than the northern crested newt in all studied countries of their co-occurrence except Romania (HARTEL *et al.* 2007; HARTEL *et al.* 2010*b*). In some study areas the northern crested newt was so rare that its habitat requirements could not be determined (e.g. DENOËL & FICETOLA 2007*a, b*).

Most studies demonstrated that both newt species avoided ponds with fish (Table 4). However, while fish presence affected negatively the northern crested newt all over its range and latitudinal gradient, such impact was not found on the smooth newt in Norway, Britain and Ireland (Table 4).

For the northern crested newt, land cover type was significant over the latitudinal gradient studied, while the aquatic requirements varied more. Ponds surrounded by cultivated land were generally avoided and those surrounded by woodland or scrub were favoured (Table 4). Among pond characteristics, the total area

Table 4. Aquatic and terrestrial habitat characteristics of the northern crested newt (*Triturus cristatus*) and the smooth newt (*T. vulgaris*), assessed in reviewed studies. P – significantly positive; N – significantly negative (*– $p < 0.05$ in logistic regression models/discriminant analyses; **– $p < 0.05$ in other type of analysis: t-test, χ^2-test, Kruskal-Wallice ANOVA, Spearman-test, etc.); 0 – no significant effect; – not measured.

Latitude	Country	Woodland near the pond	Cultivated land near the pond	Fish	Area of the pond	Max depth of the pond	Extent of open water	Vegetation cover in the pond	Water transparency/ colour	Shade	Source
The northern crested newt (*Triturus cristatus*)											
63°N	Norway	P*	N*	N*	0	–	–	0	0	N*	DOLMEN 1982, SKEI *et al.* 2006, DOLMEN *et al.* 2008
59°N	Sweden	P**	–	–	–	–	0	P**	0	N**	MALMGREN 2002, GUSTAFSON *et al.* 2006, GUSTAFSON *et al.* 2009
56°–55°N	Denmark	P*	N*	N**	0	0	0	0	P*	0	RANNAP *et al.* 2009
54°N	Lithuania	P**	–	N**	0	0	–	P**	0	P**25–50% optimal	BASTYTÉ 2008
54°N	UK, Cumbria	P**	N**	N**	0	0	N**	–	–	–	DENTON 1991
52°N	Germany	P**		–	–	–	–	–	–	–	MÜLLNER 2001
52°–51°N	UK	P* Scrub	N**	N*	P** < 80 m² avoided	P** 0.5–1 m optimal	P**	P**	–	–	COOKE & FRAZER 1976, BEEBEE 1977, 1981, 1985
51°N	The Netherlands	0	0	–	0	0	0	P*	0	0	STUMPEL 2004
48°N	France Mayenne	–	–	–	P**	P**	–	0	–	–	SCHOORL & ZUIDERWIJK 1981

Table 4 (continued)

Latitude	Country	Woodland near the pond	Cultivated land near the pond	Fish	Area of the pond	Max depth of the pond	Extent of open water	Vegetation cover in the pond	Water transparency/ colour	Shade	Source
45°N	Romania	P*	0	N*	0	–	–	P* < 60% optimal	–	–	HARTEL *et al.* 2007, HARTEL *et al.* 2010a, HARTEL *et al.* 2010b
46°–44°N	France	0	N*	N*	N*	–	–	P*	–	–	JOLY *et al.* 2001
The smooth newt (*Triturus vulgaris*)											
64°–58°N	Norway	P*	–	0	N*	–	–	0	0	–	SKEI *et al.* 2006, DOLMEN *et al.* 2008
59°N	Sweden	P**	–	–	–	–	–	–	–	–	MALMGREN 2002
56°–55°N	Denmark	0	0	N**	0	0	0	0	P*	0	RANNAP *et al.* 2009
54°N	Lithuania	0	–	N**	0	0	–	P	P**	P** 25–50% optimal	BASTYTÉ 2008
54°N	UK Cumbria	P**	N**	0	0	0	N**	–	–	–	DENTON 1991
54°–52°N	Ireland	P*	–	0	0	0	P*	0	0	–	MARNELL 1998
52°N	Germany Lower Saxony	0	–	–	–	–	–	–	–	–	MÜLLNER 2001
52°–51°N	UK	P*	N**	N**	P** < 100 m2 avoided	0	0	P** > 20% preferred	–	–	COOKE & FRAZER 1976, BEEBEE 1977, 1981, 1985

Table 4 (continued)

Latitude	Country	Woodland near the pond	Cultivated land near the pond	Fish	Area of the pond	Max depth of the pond	Extent of open water	Vegetation cover in the pond	Water transparency/ colour	Shade	Source
51°N	The Netherlands	0	0	–	0	P*> 0.5 m	0	P* > 5% preferred	P*	0	STUMPEL 2004
50°N	Belgium	0	N*	N*	P*	P*	–	–	–	–	DENOËL & FICETOLA 2007a, b
49°N	Germany Bavaria	0	–	–	0	–	–	–	–	–	MANN *et al.* 1991
45°N	Romania	0	0	N*	0	–	–	P*	–	–	HARTEL *et al*. 2007, HARTEL *et al*. 2010b
45°–44°N	Italy	P*	N*	N*	0	N*	0	P*	–	0	PAVIGNANO 1988, PAVIGNANO *et al.* 1990, FASOLA 1993, ILDOS & ANCONA 1994, FICETOLA & DE BERNARDI 2004, 2005

and depth were influential only at the lower latitudes. Vegetation cover of the pond was generally favoured all over the latitudinal gradient. Exposure to sun was particularly essential at high latitudes (Norway and Sweden; Table 4).

Habitats of the smooth newt also varied geographically. Interestingly, land cover type did not reveal any significance in the central part of the range, but forest or scrub became clearly favoured at range margins, in countries of widely varying forest cover (Norway, Sweden, UK, Ireland and Italy; Table 4). Concerning the aquatic habitat characteristics, both newt species preferred ponds rich in vegetation (unless the vegetation exceeded 1 m height; RANNAP *et al*. 2009) and with transparent water (Table 4). The smooth newt tended to occur, on average, in larger water bodies than the northern crested newt (COOKE & FRAZER 1976, MARNELL 1998, DENTON 1991, DENOËL & FICETOLA 2007*b*). Sun exposure of the pond was not important for the smooth newt (Table 4).

DISCUSSION

Geographic variation in habitat requirements

Our case study combined with the literature review supports the earlier findings that habitat characteristics of wide-ranging species do vary geographically (COLLINS 1983, GRAZYBOWSKI *et al*. 1994, CONSTIBLE *et al*. 2009). In each of the two newt species, geographical patterns were discovered in at least one key requirement, but additional patterns may have been overlooked due to methodological inconsistency of the reviewed studies. A lack of uniformity between studies (e.g. different design and methodology, different sampling units and statistical analyses conducted) did not allow using meta-analysis in our paper (see ARNQVIST & WOOSTER 1995, GATES 2002). This is very likely a common problem in wildlife habitat studies; thus, we encourage researchers to consider better standardization of methodologies to enable habitat analyses over species ranges.

In the newts, the geographic variation in habitat requirements appeared to be mostly restricted to range edges because the methodologically similar studies in the central parts of the ranges, in Denmark (RANNAP *et al*. 2009) and in Estonia, revealed large overlap. These countries are situated approximately 1000 km apart and have distinct land use (intensive in Denmark, extensive in Estonia) and length of the growing season (225 days and 180 days respectively; CHRISTENSEN 2006, Estonian State Meteorological Institute). Therefore, regional (but not necessarily local) habitat requirements should be taken into account when planning the conservation management of threatened species (see also WHITTINGHAM *et al*. 2006, CONSTIBLE *et al*. 2009).

In the northern crested newt, the distinct preference for sun-exposed water bodies in the northern part of the range at high latitudes, might be associated with the short growing season and lower temperatures limiting newt reproduction there (see LANGTON *et al*. 2001, GUSTAFSON *et al*. 2009). This was the only contrasting habitat feature for that species in Estonia (a tendency for shade avoidance) versus Denmark (no effect; RANNAP *et al*. 2009). In the northern range edge (in Norway), typical breeding waters of the northern crested newt are even situated on open bogs close to forest edge where water heats up quickly, creating favourable conditions for the development of eggs and invertebrate prey (SKEI *et al*. 2006). Also in Sweden water temperatures were significantly higher in ponds where the northern crested newt occurred (GUSTAFSON *et al*. 2009). At the same time at lower latitudes, ponds with shading (up to 60 %) were still optimal habitats for the crested newt (OLDHAMN *et al*. 2000). In the smooth newt, negative effect of shade has not been demonstrated, which can be explained by the shorter developmental time of its larvae (DOLMEN 1983).

In the smooth newt, regional variation appeared in the importance of land cover surrounding the breeding pond, while this habitat feature was essential for the northern crested newt throughout its range. For the northern crested newt, the consistent importance of forest or grassland-forest mosaic and the avoidance of cultivated fields (both in well-forested landscapes as well as where forests are patchy and isolated) have been explained with a rich microhabitat supply in forests for foraging, shelter and hibernation (JEHLE 2000, SKEI *et al*. 2006, DENOËL & FICETOLA 2007*b*), while monoculture fields lack invertebrate prey (MEEK *et al*. 2002). For the smooth newt, similar preferences for woodland and scrub generally appeared at range margins only (PAVIGNANO 1988, MARNELL 1998, BEEBEE 1981, SKEI *et al*. 2006); in northern Italy also buildings near water body were favoured (ILDOS & ANCONA 1994). In the central part of the range most of the smooth newts are known to stay just in close vicinity of the breeding pond and to use a variety of microhabitats there (MÜLLNER 2001). Thus the smooth newt appears to survive without additional hiding, foraging and hibernation sites there, which might be explained by more optimal climatic conditions.

Although the area and depth of the water bodies used by the newts also varied considerably across their ranges, this may be mostly linked to local pond supply. While small and shallow (<0.5 m) ponds were generally avoided (COOKE & FRAZER 1976, BEEBEE 1977, 1981, OLDHAM *et al*. 2000, DENOËL & FICETOLA 2007*b*), such ponds were favoured in France by the northern crested newts (JOLY *et al*. 2001) and in Norway and Italy by the smooth newts (FICETOLA & DE BERNARDI 2004, DOLMEN *et al*. 2008). The general avoidance of shallow breeding waters can be explained by their short hydroperiod, high desiccation risk, lack of prey and rapid fluctuations in temperature or oxygen content (DENOËL & FICETOLA 2007*b*). In Estonia, the smooth newt even occupied deeper ponds than the average ones available. However, in certain regions small temporary wetlands may be preferred by newts mainly due to the absence of fish (FICETOLA & DE BERNARDI 2004, DOLMEN *et al*. 2008).

Explaining the contrasting population trends of the species

Although the two newt species coexist naturally in most of their distribution area (ZUIDERWIJK 1986) and have generally similar breeding habitat preferences (e.g. COOKE & FRAZER 1976), our study indicated some substantial differences as well, which might explain the contrasting trends of those species.

First, contrarily to the northern crested newt, the smooth newt may sometimes persist in water bodies with fish (BEEBEE 1981, MARNELL 1998, SKEI *et al*. 2008), which can be explained by different larval behaviour. Larvae of the smooth newt tend to feed in the densely vegetated zone of the water body (HAGSTRÖM 1979, DOLMEN 1983), while northern crested newt's larvae are nektonic (JOLY *et al*. 2001). Tolerance for fish allows the smooth newt to use larger water bodies (DENTON 1991). While fish introduction is considered one of the most widespread anthropogenic threats to amphibians (KATS & FERRER 2003), the smooth newt may thus be able to persist in landscapes that lack fish-free breeding waters and are unsuitable for the northern crested newt.

Secondly, the smooth newt was less sensitive to shade all over its range, which may be explained by the shorter developmental time of its larvae, compared to the northern crested newt. Due to the changed land use and loss of historical function, many water bodies have become overgrown and are too shaded for northern crested newts to breed in modern landscapes. And thirdly, the surrounding land cover in general was important for the northern crested newt throughout its distribution range – a mosaic of forest and open areas (bogs, grasslands) was favoured and the cultivated fields were avoided (BEEBEE 1981, SKEI *et al*. 2006, RANNAP *et al*. 2009). For the smooth newt, the land cover type revealed important only at its range margins (PAVIGNANO 1988, MARNELL 1998, SKEI *et al*. 2006). We therefore suggest that the traits that have enabled the smooth newt to stay more abundant and persist in modern landscapes better than the northern crested newt are related to its smaller size, shorter larval period and different larval behaviour. Those traits allow the species to occupy a variety of terrestrial habitats, both open and shaded ponds and, in some conditions, even ponds containing fish.

*

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Appendix 1

Habitat characteristics measured/estimated in the 35 studies included in the review

Characteristic	Study where characteristic was measured/estimated
Soil/strata of an area	BEEBEE 1981, BEEBEE 1985, DENTON 1991
Land cover type around the pond	SCHOORL & ZUIDERWIJK 1981, PAVIGNANO 1988, PAVIGNANO *et al.* 1990, MARNELL 1998, JEHLE & ARNTZEN 2000, OLDHAM *et al.* 2000, JOLY *et al.* 2001, RANNAP *et al.* 2009
Cover or presence of forest/woodland/ scrub around the pond	BEEBEE 1977, 1981, 1985, DOLMEN 1982, PAVIGNANO 1988, DENTON 1991, MANN *et al.* 1991, ILDOS & ANCONA 1994, MARNELL 1998, JOLY *et al.* 2001, MÜLLNER 2001, MALMGREN 2002, FICETOLA & DE BERNARDI 2004, STUMPEL 2004, DENOËL & FICETOLA 2007*a*, 2007*b*, BASTYTÉ 2008, RANNAP *et al.* 2009, HARTEL *et al.* 2010*a*, 2010*b*.
Cover or presence of cultivated fields around the pond	BEEBEE 1981, DOLMEN 1982, PAVIGNANO 1988, DENTON 1991, ILDOS & ANCONA 1994, JOLY *et al.* 2001, FICETOLA & DE BERNARDI 2005, STUMPEL 2004, DENOËL & FICETOLA 2007*a*, 2007*b*, RANNAP *et al.* 2009, HARTEL *et al.* 2010*a*, 2010*b*.
Cover or presence of grassland around the pond	BEEBEE 1981, ILDOS & ANCONA 1994, MÜLLNER 2001, FICETOLA & DE BERNARDI 2004, STUMPEL 2004, HARTEL *et al.* 2010*a*, 2010*b*.
Urban cover around the pond	DENOËL & FICETOLA 2007*b*, HARTEL *et al.* 2010*a*, 2010*b*
Presence of gardens around the pond	BEEBEE 1985
Presence of bogs around the pond	MARNELL 1998
Presence of human inference around the pond	PAVIGNANO 1988, PAVIGNANO *et al.* 1990
Presence of roads around the pond	HARTEL *et al.* 2010*a*, 2010*b*
Distance from urban areas	ILDOS & ANCONA 1994
Distance to the forest/woodland	SKEI *et al.* 2006, DENOËL & FICETOLA 2007*a*, 2007*b*, BASTYTÉ 2008, HARTEL *et al.* 2010*a*, 2010*b*
Width of uncultivated buffer around the pond	JOLY *et al.* 2001, HARTEL *et al.* 2007, BASTYTÉ 2008, RANNAP *et al.* 2009
Pond density in the surroundings	MANN *et al.* 1991, JOLY *et al.* 2001, DENOËL & FICETOLA 2007*b*, HARTEL *et al.* 2010*b*
Distance to the nearest wetland occupied by conspecifics	FICETOLA & DE BERNARDI 2004, RANNAP *et al.* 2009
No. of wetlands in the surroundings of a pond	MÜLLNER 2001, FICETOLA & DE BERNARDI 2004

Characteristic	Study where characteristic was measured/estimated
Age of a pond	PAVIGNANO 1988, LAAN & VERBOOM 1990, PAVIGNANO *et al.* 1990, STUMPEL 2004
Presence of fish in the pond	BEEBEE 1981, 1985, DENTON 1991, ILDOS & ANCONA 1994, MARNELL 1998, OLDHAM *et al*. 2000, JOLY *et al*. 2001, FICETOLA & DE BERNARDI 2004, 2005, SKEI *et al.* 2006, DENOËL & FICETOLA 2007*b*, HARTEL *et al*. 2007, BASTYTÉ 2008, RANNAP *et al*. 2009, HARTEL *et al*. 2010*a*
Pond area	COOKE & FRAZER 1976, BEEBEE 1977, SCHOORL & ZUIDERWIJK 1981, PAVIGNANO 1988, DENTON 1991, MANN *et al*. 1991, ILDOS & ANCONA 1994, MARNELL 1998, JOLY *et al*. 2001, FICETOLA & DE BERNARDI 2004, STUMPEL 2004, GUSTAFSON *et al*. 2006, DENOËL & FICETOLA 2007*b*, DOLMEN *et al*. 2008, RANNAP *et al*. 2009, HARTEL *et al*. 2010*b*
Maximum depth of the pond	COOKE & FRAZER 1976, BEEBEE 1981, SCHOORL & ZUIDERWIJK 1981, PAVIGNANO 1988, PAVIGNANO *et al.* 1990, DENTON 1991, FASOLA 1993, ILDOS & ANCONA 1994, MARNELL 1998, FICETOLA & DE BERNARDI 2004, STUMPEL 2004, GUSTAFSON *et al*. 2006, DENOËL & FICETOLA 2007*b*, BASTYTÉ 2008
Water permanence of the pond	FICETOLA & DE BERNARDI 2004, 2005
Sediment in the pond	ILDOS & ANCONA 1994, BASTYTÉ 2008, RANNAP *et al*. 2009
Water transparency/colour	ILDOS & ANCONA 1994, MARNELL 1998, STUMPEL 2004, SKEI *et al.* 2006, BASTYTÉ 2008, GUSTAFSON *et al*. 2009, RANNAP *et al*. 2009
Percentage of open water	COOKE & FRAZER 1976, PAVIGNANO 1988, DENTON 1991, MARNELL 1998, STUMPEL 2004, HARTEL *et al*. 2007, RANNAP *et al*. 2009
Cover of water vegetation	BEEBEE 1977, 1981, SCHOORL & ZUIDERWIJK 1981, PAVIGNANO 1988, PAVIGNANO *et al.* 1990, MARNELL 1998, JOLY *et al*. 2001, STUMPEL 2004, GUSTAFSON *et al*. 2006, SKEI *et al*. 2006, HARTEL *et al*. 2010*a*
Cover of floating vegetation	ILDOS & ANCONA 1994, JOLY *et al*. 2001, FICETOLA & DE BERNARDI 2004, BASTYTÉ 2008, RANNAP *et al. 2009*
Cover of tall vegetation in the pond	RANNAP *et al*. 2009
Cover of submerged vegetation	ILDOS & ANCONA 1994, FICETOLA & DE BERNARDI 2004, BASTYTÉ 2008, RANNAP *et al*. 2009
No. of plant species in the pond	GUSTAFSON *et al*. 2006
Plants suitable for egg-laying	MIAUD 1995
Favored species of water vegetation	STRIJBOSCH 1979
Invertebrate diversity of the pond	RANNAP *et al*. 2009
Steepness of pond slopes	ILDOS & ANCONA 1994, FICETOLA & DE BERNARDI 2004, BASTYTÉ 2008, RANNAP *et al*. 2009
Width of the shallow-water zone	BASTYTÉ 2008, RANNAP *et al*. 2009
Sun exposure/water temperature of the pond	STUMPEL 2004, FICETOLA & DE BERNARDI 2004, 2005, SKEI *et al.* 2006, BASTYTÉ 2008, GUSTAFSON *et al*. 2009, RANNAP *et al*. 2009
Presence of dead wood around the pond	MARNELL 1998