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Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats

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ABSTRACT

1. Amphibians are declining worldwide in response to local and global pressures. Pond-breeding species are particularly vulnerable to environmental change because they rely on two components of the landscape: aquatic and terrestrial habitats. Agricultural practices are changing rapidly at world and local scales. As a consequence, farm ponds and their surrounding terrestrial landscapes will probably be affected.
2. This study investigated the main habitat determinants for the occurrence of four species of newts (genus *Triturus*) inhabiting the Pays de Herve, a rural area in Belgium. Newt occurrence was determined for 258 ponds and the effect of habitat on distribution determinants was evaluated using generalized linear models.
3. Newts were found in 42% of the ponds. Contrary to expectations, the distribution of newts was not positively associated with a high density of ponds. However, a low occurrence of newts and the low water depth of many ponds suggest a low quality of habitats. Proximity to forest, deep water, and an absence of fish in ponds are factors that significantly favour newts, but terrestrial habitat requirements vary among species.
4. These results indicate the necessity of maintaining both forest and meadow patches in close proximity to ponds inhabited by newts, and of controlling fish introduction in those ponds. These findings stress the importance of conservation and management of terrestrial and aquatic habitats for maintaining amphibian diversity.
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KEY WORDS: amphibians; decline; fish introduction; fragmentation; habitat determinants; landscape use; metapopulation

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INTRODUCTION

Amphibians are representative of the current biodiversity decline at a world scale (Semlitsch, 2003a; Stuart *et al*., 2004). Many amphibian species require both terrestrial and aquatic habitats during their life cycle, which makes them particularly vulnerable to a large range of detrimental factors (Alford *et al*., 2001; Semlitsch, 2003b). In a recent review, Collins and Storfer (2003) reported five main causes of amphibian decline: introduction of alien species, habitat alteration, over-exploitation, global change and infectious diseases.

Deterioration of landscape structure occurs at both local and global scales and can affect a large number of organisms. It is expected that 10^9 ha of natural ecosystems will be converted to agriculture by 2050 (Tilman *et al*., 2001). Although at first agriculture and some other human activities initially favoured amphibian diversity by creating a large variety of water bodies, a direct consequence of the increase of cultivation is now a decrease of forest extent and number of ponds. Pond-breeding amphibians are particularly likely to suffer directly from landscape cultivation because they lose breeding sites (ponds) and suitable post-larval and post-breeding terrestrial habitats (Herbeck and Larsen, 1998; Beja and Alcazar, 2003). In the past century, 75% of ponds have been lost in Great Britain, with some areas losing up to 95% of ponds (Wood *et al*., 2003). In addition, habitat destruction increases fragmentation and pond isolation. This may affect amphibian populations because of their metapopulation structure and their usually short migration distance (Laan and Verboom, 1990; Miaud, 1990; Joly *et al*., 2001; Ficetola and De Bernardi, 2004). However, this remains controversial because the dispersal abilities of amphibians may not be as limited as has often been suggested (Marsh and Trenham, 2001).

The introduction of alien species has serious consequences for native amphibians (Hecnar and M'Closkey, 1997; Kats and Ferrer, 2003; Kiesecker, 2003; Denoël *et al*., 2005; Knapp, 2005; Orizaola and Braña, 2006). Laboratory studies have confirmed the detrimental effect of alien species when they are predators and competitors of amphibians (Gamradt and Kats, 1996; Smith *et al*., 1999). Fish (Knapp, 2005), bullfrogs (Lawler *et al*., 1999) and crayfish (Cruz and Rebelo, 2005) have been implicated as major contributors to amphibian decline. Although fish introduction is usually the result of isolated actions, it is a worldwide threat to amphibians because of thousands of such introductions in numerous countries (Kiesecker, 2003).

Multiple, concomitant factors, inducing the decline of amphibians, as well as economic factors make landscape management a difficult task. Therefore, in recent years, many studies have investigated the relationships between amphibian distribution and habitat features in building quantitative models from a management perspective (Vos and Stumpel, 1995; Ray *et al*., 2002; Porej *et al*., 2004; Knapp, 2005; Rubbo and Kiesecker, 2005). Ideally these studies should take into account a large number of possible factors that act at different spatial scales. Very large data sets are required to test the contemporary effect of numerous factors, since model reliability is high only when the ratio of the number of sites to the number of factors is large (Rushton *et al*., 2004). Therefore, some studies focused only on one or a few factors, such as the wetland features, the composition of landscape (i.e. the amount of landscape covered by a given land-use) or the configuration of landscape (i.e. the spatial features of landscape such as isolation and shape of patches) (e.g. Marsh and Trenham, 2001; Guerry and Hunter, 2002) and more studies are required to evaluate the relative role of these components. Two recent reviews found that only a small number of studies on amphibians are performed at landscape level: most of the studies are patch-based, sometimes with little replication (McGarigal and Cushman, 2002; Cushman, 2006). Ultimately, both patch and landscape level studies are necessary to understand the effects of habitat alteration on species (Denoël and Lehmann, 2006).

In northern Europe, newts (genus *Triturus*) are widespread across a large range of habitats (Griffiths, 1996). *Triturus* newts live in water during their larval stage and for reproduction but they are generally terrestrial for the rest of the year. Four of the five newt species of northern Europe are present in Belgium

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(Parent, 1997). *Triturus cristatus* is particularly threatened and is the rarest newt species in Belgium. By its inclusion in annex II of the European Habitats Directive, *T. cristatus* receives a level of protection that requires the designation of protected areas. These sites will form part of the pan-European network known as Natura 2000 (Clemons, 1997). A clear understanding of the habitat requirements of these species is a necessary prerequisite to assessing their conservation status and to plan management. Effective conservation of newts will require an understanding of their conservation needs both at the pond and the landscape level.

Recent studies have shown that the genus *Triturus* is paraphyletic (e.g. Weisrock *et al*., 2006), so it may be split in the near future into three genera: *Mesotriton* for *T. alpestris*, *Lissotriton* for the small-bodied species and *Triturus* for the large-bodied species, according to the suggestion of Garcia-Paris *et al*. (2004). However, in the absence of taxonomic agreement the traditional nomenclature will be used in the present paper.

The aim of this study was to determine the habitat features influencing the occurrence of the four newt species (*Triturus alpestris*, *T. cristatus*, *T. helveticus* and *T. vulgaris*) in an agricultural area of Belgium (Pays de Herve). This area supports livestock farming but is increasingly used for agricultural cultivation and extension of urban areas. Detrimental effects on wilderness, specifically on amphibians, are therefore expected to occur. The study area is an example of the current trend of environmental change in Europe (Stoate *et al*., 2001; Wood *et al*., 2003). Two hundred and fifty-eight ponds and surrounding landscapes were analysed by statistical techniques designed to take into account spatial structure. This procedure allowed simultaneous testing of the effect of a large number of factors that potentially influence newt distribution, including the wetland features, the composition of landscape, and the isolation of wetlands in relation to terrestrial habitat used during the post-breeding season. The integration of these different levels of analysis allows us to propose specific procedures of habitat conservation and management to improve the persistence of the newt guilds in farmland landscapes.

MATERIALS AND METHODS

Study site and sampling procedures

The study site (Pays de Herve *sensu lato*) is a farmland area (mainly livestock) in eastern Belgium. Most of the land is occupied by meadows, with some crop fields and patches of forest present. It is bordered by two large rivers to the west (Meuse River) and south (Vesdre River) and reaches the Netherlands and German borders to the north and the German border to the east (from 5° 34′ E to 6° 11′ E longitude and 50° 33′ N to 50° 46′ N latitude). The Pays de Herve covers an area of 614 km^2 and includes 1934 ponds (Denoël, 2004a). Most of the ponds are man-made and were initially used to water cattle. Because of this use, but also because of the fresh and rainy weather of Belgium (see, for example, Müller, 1996), most ponds retain water during the whole reproductive period of newts.

Three hundred and seventy-one different ponds were sampled between 1990 and 2004 during the active breeding period of newts (February–July); only 258 ponds are included here because of incomplete data sets for some of the sites. Each pond was sampled at least once during the peak of the reproductive season to maximize the chance of finding newts. Ponds were found on the basis of very accurate local topographic maps (Institut Géographique National, 1:10 000 and 1:25 000), which indicate even the smallest water bodies, and cover all the Pays de Herve (Figure 1). Streams were not analysed here because most streams in Pays de Herve are not suitable for newts (Denoël, 2004a). Newt and fish presence were determined by repeated dip-netting of the ponds (mesh size: 4 mm). The presence of a newt species was assessed by the capture of either adults or larvae. Because of mud and leaves, even small larvae can be caught with this net. Absence of a species was only concluded after numerous attempts at dip-netting (i.e. several dozen sweeps

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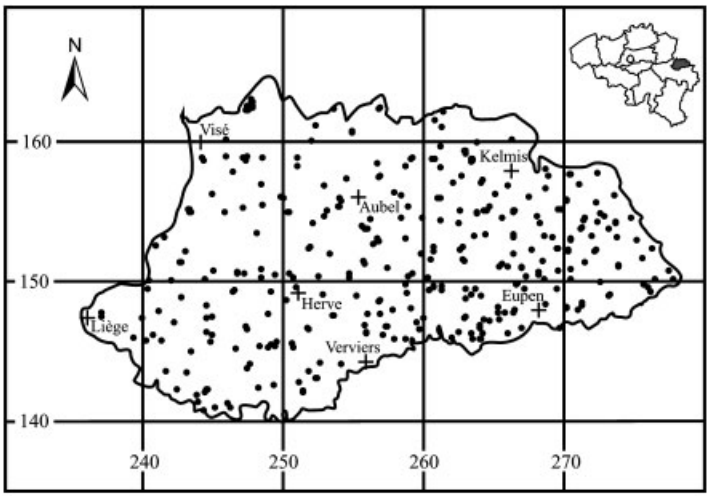

Figure 1. Location of the study sites ($n = 258$) in Pays de Herve (Belgium). Coordinates: Lambert Grid (10×10 km).

of the net) were undertaken in all favourable areas of a pond. Both vegetation and open areas were intensively searched for the presence of newts. Although it is possible that one or more species may have been missed in some ponds, the absence of a record indicates that the species is very rare in that pond and suggests that this would at best be a 'sink' or transient habitat (Perret *et al*., 2003). We therefore believe that our approach is sufficiently robust to allow an unbiased association of species with environmental variables. Interviews of local owners were held to receive data on fish introductions. Pond area and maximum pond depth were measured at each site.

Habitat characterization

To evaluate the landscape composition, topographical maps were analysed to measure: (1) pond density within a 400-m (i.e. 50 ha) radius centred at each pond, since this is the average migration distance of newts (Joly *et al*., 2001); (2) the forest cover percentage within 50 ha, because wooded areas are a favourable terrestrial habitat for newts outside the reproductive period (Griffiths, 1996; Schabetsberger *et al*., 2004; Denoël and Ficetola, 2007); (3) the percentage of cultivated lands (i.e. crops: mainly cereals); and (4) the extent of urban area within the 50 ha because these areas may not be suitable as terrestrial habitat (Joly *et al*., 2001; Pellet *et al*., 2004; Rubbo and Kiesecker, 2005). Forest and crop cover percentages were measured by topographic maps. It was impossible to measure percentage cover precisely for urban areas because buildings can be small and very numerous at the scale studied, so urban cover was measured by dividing the 50 ha area into 16 equal sections and checking for the presence of buildings in each of the sections. Therefore, urban cover was estimated using a rank scale with a minimum value of zero (no building within 50 ha) and a maximum value of 16 (buildings in all the sectors). As a measure of landscape configuration (isolation of breeding areas from the terrestrial habitat), the distance from each pond to the edge of the closest forest was measured. The presence of fish was recorded and the area and maximum depth of water during the reproductive period of newts was measured. No additional variables were chosen to maintain a large ratio between the number of variables and the number of ponds. This is not expected to affect the results because the seven variables used are representative of the landscape in Pays de Herve, in which the main classes of habitats are rather homogeneous.

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Statistical analysis

Generalized linear models (GLMs) were used to relate newt occurrence and diversity to environmental features. Pairwise correlation were calculated among variables to evaluate the presence of multicollinearity. In large data sets, multicollinearity can pose difficulties when the pairwise $|r|$ between two variables is $\geqslant 0.8$ (Berry and Feldman, 1985; Bowerman and O'Connell, 1990). However, no strong pairwise correlations were found between variables (Table 1). The strongest pairwise correlation was between forest cover and distance to forest ($r = -0.738$).

GLMs assuming binomial error distribution (logistic regression) were used to relate the distribution of environmental features to each newt species. Similarly, a Poisson error distribution (Poisson regression) was assumed to relate the number of species found at a pond with the environmental features. All possible models including only significant variables were built and their relative performance was evaluated using the Akaike's Information Criterion (AIC) (Mazerolle, 2006). All models differing by less than two AIC units from the best model were considered as candidate models (Mazerolle, 2006). More than a single candidate model was obtained only for *T. alpestris*. In all other cases, only the best model according to AIC was shown. The significance of terms was tested by a likelihood ratio test. As a measure of the fit of the models the Nagelkerke's r^2 (r^2_{N}), which measures the proportion of variance explained by the model, was used (Nagelkerke, 1991).

In all models the residual deviance was lower than or similar to the residual degrees of freedom. Therefore, data were not over-dispersed, suggesting that the error structure was appropriate for the data and that predictors were appropriate to describe the data set (Rushton *et al.*, 2004). The maximum number of predictors retained per model was five; since the dataset included 258 ponds, in all models the number of observations was > 50 times the number of predictors so the results can be assumed to be reliable (Rushton *et al.*, 2004). Cook's distances were used to evaluate the presence of cases having an undue influence on the models. Since all Cook's distances were well below 1, we assumed that our models were not unduly influenced by a few cases (Bowerman and O'Connell, 1990).

The robustness of the logistic and Poisson models was evaluated using a jackknife procedure. A sample of n wetlands was removed from the data set in turn and the model coefficients were estimated using the remaining data; this procedure was repeated $258/n$ times. Two different sample sizes of n were used: 10 and 25 ponds.

These data are spatially structured points, therefore spatial autocorrelation of observations could potentially bias the results of the analysis. Moran I was used to evaluate the spatial autocorrelation of residuals of GLMs following the Monte Carlo procedure described by Lichstein *et al.* (2002). In the logistic

Table 1. Pairwise correlations among variables

		Depth	Fish	*n* ponds	Crop%	Forest%	Urban cover	Distance to forest
Area	*r*	0.592	0.478	−0.010	−0.101	0.073	0.110	−0.318
	p	0.000	0.000	0.870	0.107	0.243	0.078	0.000
Depth	*r*		0.316	0.080	−0.042	−0.014	0.104	−0.143
	p		0.000	0.203	0.500	0.818	0.096	0.022
Fish	*r*			0.053	−0.074	0.065	0.120	−0.176
	p			0.395	0.233	0.298	0.054	0.004
n ponds (50 ha)	*r*				−0.047	−0.147	0.038	0.110
	p				0.448	0.018	0.547	0.078
Crop% (50 ha)	*r*					−0.232	−0.117	0.191
	p					0.000	0.061	0.002
Forest% (50 ha)	*r*						−0.376	−0.738
	p						0.000	0.000
Urban cover (50 ha)	*r*							0.250
	p							0.000

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regression models residuals were not spatially autocorrelated (all $p > 0.15$); therefore we assumed that autocorrelation is not a major bias in these models. In the Poisson model (relationship between species richness and habitat features), a weak but significant spatial autocorrelation of residuals was found (Moran $I = 0.074$, $p = 0.04$). The reliability of this regression model was assessed using a spatial simultaneous autoregressive lag model estimation (lagSAR). LagSAR includes a maximum likelihood estimation of the spatial autoregressive coefficient rho in multiple regression models. This model is therefore suitable to evaluate the relationships between species distribution and environmental features in situations in which spatial autocorrelation may bias the results of regression (Anselin, 2001). However, the results of LagSAR were extremely similar to those obtained using the Poisson regression, suggesting that spatial autocorrelation was not a major bias to this analysis. In the results section, the significance of independent variables assessed using both the Poisson GLM and the lagSAR methods were reported.

Variables were transformed using square-root (number of ponds within 50 ha; water depth; count data in the lagSAR model), natural logarithms (distance to forest; pond area) or arcsine-square root (all percentage data) to meet the assumptions of parametric analyses (Sokal and Rohlf, 1995). Regression analyses were performed using the package Car 1.0–17 (Fox, 2005) and spatial analyses using spdep 0.3–12 (Bivand, 2005). All analyses were performed under the R 2.1 environment (R Development Core Team, 2005).

RESULTS

Triturus vulgaris and *T. alpestris* were the most abundant species, with 27.1% and 26.4% of the ponds occupied by each of them, respectively. *Triturus helveticus* occupied 7.8% of ponds and *T. cristatus* occupied only 4.7% of ponds. The occurrence of these species in the different habitats is shown in Table 2. Significant models for the distribution of all species and for species richness were built. Logistic regression models for *T. alpestris* and *T. cristatus* explained only a limited proportion of variance (10–14%), while the logistic model for *T. helveticus* explained a substantial proportion of variance (44%). In all models, the coefficients obtained using the jackknifed models were similar, and their range never included zero, suggesting that these results are robust (Tables 3 and 4).

Species level analysis: pond features

For *T. alpestris*, two logistic regression models showed almost identical AIC (the difference between the best and the second-best model was 0.003 AIC units; Table 3). In this case, the AIC does not allow an unambiguous evaluation of which is the best model. The two models are very similar and therefore not difficult to interpret: they show that *T. alpestris* was observed more frequently in deep ponds and in ponds without fish.

Triturus cristatus was significantly associated with deep wetlands (Table 3). It is likely that the scarcity of this species precluded the discovery of other significant relationships. *Triturus helveticus* was significantly related to deep wetlands devoid of fish (Table 3). Similarly, *T. vulgaris* was significantly related to large, deep wetlands devoid of fish (Table 3).

Species level analysis: landscape features

Distance from the nearest forest significantly affected the distribution of *T. alpestris*, *T. helveticus* and *T. vulgaris*. *Triturus alpestris* and *T. helveticus* were negatively related to the distance from the nearest forest while, conversely, *T. vulgaris* was more frequently present in ponds far from the forest. None of the analysed landscape variables significantly affected the distribution of *T. cristatus*. The distribution of *T. vulgaris* was negatively related to the urban cover within 50 ha. The distribution of *T. helveticus* was negatively related to the crop cover within 50 ha. The presence of only one species was significantly related

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Table 2. Characteristics of habitats used and not used by newts: means ± SE (range)

	T. alpestris		*T. cristatus*		*T. helveticus*		*T. vulgaris*		*Triturus* guild	
	Presence $n = 68$	Absence $n = 190$	Presence $n = 12$	Absence $n = 246$	Presence $n = 20$	Absence $n = 238$	Presence $n = 70$	Absence $n = 188$	Presence $n = 107$	Absence $n = 151$
Area (m^2)	267 ± 57	525 ± 94	368 ± 113	461 ± 74	272 ± 78	472 ± 77	572 ± 165	414 ± 77	458 ± 109	456 ± 94
Depth (cm)	71 ± 5.1	57 ± 3.1	96 ± 13	59 ± 2.7	78 ± 12	59 ± 2.7	76 ± 4.4	55 ± 3.2	74 ± 4.1	52 ± 3.3
Fish	0.03 ± 0.02	0.12 ± 0.02	0.08 ± 0.08	0.09 ± 0.02	0.00 ± 0	0.10 ± 0.02	0.06 ± 0.03	0.11 ± 0.02	0.04 ± 0.02	0.13 ± 0.03
n ponds (50 ha)	2.88 ± 0.30	2.91 ± 0.16	3.42 ± 0.51	2.87 ± 0.15	1.90 ± 0.49	2.98 ± 0.15	3.10 ± 0.26	2.82 ± 0.17	2.93 ± 0.23	2.87 ± 0.18
Crop% (50 ha)	0.05 ± 0.01	0.06 ± 0.01	0.04 ± 0.03	0.06 ± 0.01	0.01 ± 0.01	0.06 ± 0.01	0.05 ± 0.01	0.06 ± 0.01	0.05 ± 0.01	0.06 ± 0.01
Forest% (50 ha)	0.21 ± 0.03	0.12 ± 0.02	0.07 ± 0.03	0.15 ± 0.02	0.42 ± 0.07	0.12 ± 0.01	0.10 ± 0.02	0.16 ± 0.02	0.19 ± 0.03	0.12 ± 0.02
Urban cover[a] (50 ha)	4.79 ± 0.46	5.96 ± 0.24	6.25 ± 1.10	5.62 ± 0.22	4.15 ± 0.85	5.78 ± 0.22	4.81 ± 0.38	5.96 ± 0.26	4.86 ± 0.35	6.21 ± 0.27
Distance to forest (m)	176 ± 30	283 ± 21	383 ± 134	249 ± 17	26 ± 15	274 ± 18	232 ± 29	264 ± 21	214 ± 27	284 ± 23

[a] Urban cover was measured using a rank scale (see 'Methods').

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Table 3. Logistic regression models. For *Triturus alpestris*, two models are reported since they have similar AIC

	Variables	$B \pm$ SE	χ^2	p	Jackknifed coefficients (range)		r^2_N	AIC
					Group size = 10	Group size = 25		
Triturus alpestris Model 1	Forest%	1.451 ± 0.469	9.456	0.002	1.20/1.75	1.25/1.95	0.141	279.449
	Depth	0.196 ± 0.057	12.658	0.0004	0.19/0.22	0.18/0.22		
	Fish	−2.24 ± 0.796	12.186	0.0004	−2.97/−2.05	−2.98/−1.98		
Triturus alpestris Model 2	Distance to forest	−0.176 ± 0.060	9.454	0.002	−0.20/−0.15	−0.24/−0.15	0.141	279.452
	Depth	0.173 ± 0.057	9.831	0.002	0.16/0.19	0.16/0.19		
	Fish	−2.377 ± 0.804	13.582	0.0002	−3.11/−2.19	−3.19/−2.06		
Triturus cristatus	Depth	0.303 ± 0.111	7.937	0.005	0.25/0.38	0.26/0.37	0.097	93.129
Triturus helveticus	*n* ponds	−1.094 ± 0.376	9.562	0.002	−1.30/−0.93	−1.64/−0.96	0.444	99.443
	Crop%	−4.897 ± 2.459	5.528	0.019	−5.61/−4.39	−6.42/−3.57		
	Distance to forest	−0.522 ± 0.120	26.754	<0.0001	−0.60/−0.48	−0.69/−0.44		
	Depth	0.249 ± 0.102	6.486	0.011	0.17/0.32	0.19/0.37		
	Fish	−7.538 ± 6.381	12.389	0.0004	−7.86/−6.18	−8.60/−6.27		
Triturus vulgaris	Urban cover	−0.168 ± 0.052	11.705	0.0006	−0.20/−0.15	−0.18/−0.15	0.215	272.148
	Distance to forest	0.186 ± 0.072	7.152	0.007	0.16/0.22	0.13/0.23		
	Depth	0.251 ± 0.070	13.946	0.0002	0.22/0.28	0.22/0.29		
	Area	0.242 ± 0.116	4.498	0.033	0.21/0.33	0.18/0.32		
	Fish	−1.625 ± 0.649	7.353	0.007	−2.16/−1.43	−2.22/−1.28		

Table 4. Relationship between species richness and environmental features: results of Poisson multiple regression and spatial simultaneous autoregressive lag model estimation

Variables	$B \pm$ SE	χ^2	p (GLM)[a]	p (lagSAR)[b]	Jackknifed coefficients (range)		AIC	r^2_N
					Sample size = 10	Sample size = 25		
Crop%	−0.493 ± 0.182	6.681	0.010	0.030	−0.59/−0.44	−0.61/−0.35	535.75	0.272
Urban cover	−0.027 ± 0.009	9.482	0.002	0.0004	−0.03/−0.02	−0.04/−0.02		
Depth	0.073 ± 0.011	35.785	<0.0001	<0.0001	0.07/0.08	0.07/0.08		
Fish	−0.417 ± 0.114	12.739	0.0004	<0.0001	−0.56/−0.37	−0.58/−0.32		

[a] Estimated using a Poisson general linear model.
[b] Estimated using a spatial simultaneous autoregressive lag model estimation.

to the number of ponds within 50 ha (Table 3): the probability of occurrence of *T. helveticus* was lower in high pond density areas.

Guild level analysis

Guild richness was negatively related to the presence of fish, crops and surrounding urban areas while positively related to water depth (Table 4). Fish presence strongly reduced the richness of communities: the

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average species richness of newt communities was 0.7 (SE = 0.06) species in fish-free ponds and 0.29 (SE = 0.14) in fish-inhabited ponds. Moreover, the richest communities were found in deep ponds and in ponds surrounded by landscape devoid of large arable fields and urban zones. Ponds with at least one newt species had a mean depth of 74 cm (SE = 4) whereas ponds without newts had a mean depth of 52 cm (SE = 3).

DISCUSSION

This study shows that variables occurring at both pond and landscape scales influence the occurrence and diversity of the four newt species present in the study area, Pays de Herve. Several variables, such as fish presence, water depth and distance from the nearest forest, can explain newt distribution. However, it is clear that the response to habitat characteristics differs among the four species. Therefore, despite obvious similarities among these closely related species there are notable ecological differences among them. Consequently, areas that are optimal for some species are suboptimal for others. This effect is particularly evident for the landscape features whereas the response to pond features is more consistent among species (see below).

Pond features

A strong, negative effect of fish was observed on the presence and breeding pond diversity of three newts (*T. alpestris*, *T. helveticus* and *T. vulgaris*). *T. helveticus* has been found only once in a pond inhabited by fish (*Gasterosteus aculeatus*). Although well reported in the USA (e.g. Hecnar and M'Closkey, 1997; Knapp *et al*., 2001; Knapp, 2005), the negative relationship between the presence of fish and newts has not been well investigated in Europe (e.g. Denoël *et al*., 2005). Locally in France (Joly *et al*., 2001; Denoël and Lehmann, 2006), Italy (Ficetola and De Bernardi, 2004), Portugal (Beja and Alcazar, 2003) and Spain (Orizaola and Braña, 2006), fish have been shown to be negatively associated with the presence of newts. There is expected to be a negative effect of large predatory fish (e.g. trout) and small ornamental fish (e.g. gold fish and mosquitofish) on newts and salamanders since experimental studies have shown that fish can decrease urodeles' survival (Gamradt and Kats, 1996; Tyler *et al*., 1998; Smith *et al*., 1999; Monello and Wright, 2001). Whereas the largest predators forage on both adults and larvae, gape-limited fish eat eggs and larvae. Fish also consume invertebrates (the food of newts) and disturb natural pond ecosystems, which may then become unsuitable for predatory amphibians (Schabetsberger *et al*., 2006).

Water depth affected the distribution of all newt species in Pays de Herve. Although some newt populations have been found in low water depths, shallow ponds are generally unsuitable for newts, particularly those less than 20 cm deep. Potential causes of unsuitability include risk of drying, prey scarcity, rapid variation of abiotic variables (e.g. temperature, oxygen) or disturbance, but the relative roles of these factors remain to be determined. The detrimental effect of low water depth is most probably typical of open farmland landscapes (Joly *et al*., 2001; Ficetola and De Bernardi, 2004; this study) because in other habitats, such as forests and mountains, newts are frequently found in shallow waters, such as ruts, ditches or fountains (Denoël, 2004b, in press). In Mediterranean farmland areas, they can also take advantage of temporary waters which are devoid of fish (Beja and Alcazar, 2003; Ficetola and De Bernardi, 2004) but even in such habitats very shallow waters may not be occupied by newts if they have a short hydroperiod (Denoël and Lehmann, 2006).

In agreement with Oertli *et al*. (2002), no relationship between pond size and amphibian diversity was found. Large ponds did not support a higher species richness than the small ponds and only *T. vulgaris* was more frequently observed in the larger ponds.

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Landscape features

Landscape features are expected to influence strongly the distribution of ponds occupied by newts because all four species require suitable terrestrial habitats for the post-breeding season (Griffiths, 1996). However, as shown in other studies (e.g. Guerry and Hunter, 2002; Gray *et al*., 2004; Porej *et al*., 2004; Denoël and Ficetola, 2007), the landscape requirements are different across species (Table 2). Landscape composition and configuration were strongly related, making it difficult to disentangle their relative role. Despite this limitation, it is clear that landscape configuration (e.g. the distance of ponds from the forest) is extremely important for some of the species studied.

Two species were strongly dependent on forest presence in the landscape, so both distance from the nearest forest and forest extent are likely to play a pivotal role in their distribution. *Triturus helveticus* was never observed in ponds farther than 225 m from the nearest forest, and 75% of ponds occupied by *T. helveticus* were within the forest; therefore distance from forest is extremely important for this species. For *T. alpestris*, two alternative candidate models suggested that ponds inhabited by this species were close to the forest and with a high percentage of surrounding forest (Table 2). The two models had very similar AIC, therefore it is very difficult to evaluate which model is the better one. Forest percentage and distance to the nearest forest are strongly correlated ($r = -0.738$), and wetlands close to the forest also have a high forest cover; overall, both models strongly support the importance of forest for this species. For *T. alpestris*, the average distance of occupied ponds to the forest was 176 m, and 75% of occupied ponds were less than 250 m from the forest edge. Forest is extremely important as post-breeding habitat for newts: leaf litter and dead wood are used as shelter and as hibernation sites, and in leaf litter the newts can find food (van Gelder and Grooten, 1992; Marnell, 1998; Jehle, 2000; Schabetsberger *et al*., 2004; Marty *et al*., 2005). Although it can occupy open areas, *T. helveticus* is one of the newt species typically associated with wooded environments (De Fonseca, 1982; Denoël and Lehmann, 2006; Denoël and Ficetola, 2007). Therefore, the conservation of terrestrial, forested habitat is necessary for these species. The results from the present study corroborate the importance of forest in the core zone around breeding ponds of amphibians (Hecnar and M'Closkey, 1998; Houlahan and Findlay, 2003; Porej *et al*., 2004; Marty *et al*., 2005) and confirm that buffer zones of at least 150–300 m around the wetlands are necessary for the conservation of semi-aquatic species (Semlitsch, 1998; Semlitsch and Bodie, 2003, Schabetsberger *et al*., 2004).

The presence of human-exploited landscape was negatively associated with the presence of three species (crops for *T. alpestris* and *T. helveticus* and crops and urban areas for *T. vulgaris*) and the guild richness. Landscape exploitation would be expected to affect newt occurrence, as it reduces the availability of terrestrial habitat and landscape connectivity (Pavignano *et al*., 1990; Joly *et al*., 2001; Beja and Alcazar, 2003; Rubbo and Kiesecker, 2005). The fact that newt occurrence is dependent on the proximity of forest (Denoël and Ficetola, 2007; this study) demonstrates that when forests are converted to cultivated lands newts will be affected because they will lose suitable terrestrial shelter. In addition to terrestrial habitat loss, the transition from grazed to cultivated lands is associated with a loss of breeding sites because ponds are no longer used to water cattle. Long-term longitudinal surveys are needed to model the pattern of pond extinction after land-cover change. This was not the aim of this study, but reading of topographical maps indicates that some ponds have already disappeared, particularly in areas with large cultivated lands (Denoël, 2004a).

A decrease in the density of aquatic habitats is believed to have an indirect effect on amphibian populations (Laan and Verboom, 1990; Joly *et al*., 2001). Theoretical models suggest that a low density of patches on the landscape reduces the possibility of persistence of populations and related subpopulations (Hanski and Ovaskainen, 2000; but see Sheffer *et al*., 2006). Therefore we expect that pond frequency in the immediate landscape influences metapopulation dynamics. A large density of ponds can be of primary importance in case of habitat deterioration followed by local population crashes. Low inter-pond distances favour dispersal and migration of newts from unfavourable sites and thus the continued presence of newts

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at a local scale. Field studies have confirmed the negative effects of pond isolation on amphibian occurrence (Oldham *et al*., 2000; Joly *et al*., 2001; Ficetola and De Bernardi, 2004; Gray *et al*., 2004). However, in our study, no significant positive effect of pond density was found, either for species presence or for guild richness. One species (*T. helveticus*) was even more frequently observed in areas with low pond density, a result difficult to explain on the basis of metapopulation theory. Consequently, the difference between studies is probably partly due to differences in landscape and habitat quality. Indeed, surrounding ponds do not represent necessarily attractive habitats (for example, because of the presence of predators, a low depth, or any other detrimental characteristic). For instance, newt occurrence was almost twice as high in Dombes (78.5%; Joly *et al*., 2001) than in Pays de Herve (42%; this study), which indicates that ponds from Pays de Herve may be less suitable to newts. In support of these arguments, Denoël and Lehmann (2006) showed that *T. helveticus* populations in Larzac (southern France) were smaller in breeding sites surrounded by many ponds but higher in integrating the adequacy of surrounding ponds in the models. Moreover, in less isolated wetlands interspecific interactions can be stronger than in isolated water bodies and may have complex consequences on the populations. Species negatively affected by such interactions are predicted to be less frequent in the less isolated wetlands (Sheffer *et al*., 2006). Detailed studies at the scale of individual ponds would be helpful for understanding these patterns, but gathering a large number of detailed longitudinal data per site would be a difficult task across a large number of ponds (see, for example, Angelibert *et al*., 2004; Marty *et al*., 2005).

There is continuing debate about the relative role of reduction of habitat quantity (i.e. changes in landscape composition) and increased isolation of patches (i.e. changes in landscape configuration) for the conservation of biodiversity. In her review of the effects of fragmentation processes, Fahrig (2003) found that the loss of habitat has stronger effects on biodiversity than the increased isolation of patches, suggesting that habitat quantity is the main landscape feature that should be conserved for biodiversity. Our study observed a different pattern. For *T. helveticus*, the role of forest proximity appeared to be more important than forest abundance; for *T. alpestris* the two variables appeared to play an equally important role. Because of limited dispersal capability, most semiaquatic amphibians, including newts, require suitable terrestrial habitats in close proximity to wetlands (Miaud, 1990; Semlitsch, 1998; Gibbons, 2003; Schabetsberger *et al*., 2004). An increased risk of extinction in populations far from suitable habitats has been observed for other newt species (Griffiths and Williams, 2000; Ficetola and De Bernardi, 2004). Such species can therefore be extremely sensitive to the negative effects of isolation between ponds and terrestrial habitats (Guerry and Hunter, 2002). Most studies that report a limited effect of isolation on biodiversity have been performed on birds, on flying insects and on other species with high dispersal capability (Fahrig, 2003). It is likely that the effects of isolation on less mobile species would be more negative, particularly when the species require two different habitats for survival.

Management implications

Triturus cristatus — the only local newt species listed in the Habitats Directive — appeared to be very rare in Pays de Herve, with an occurrence of only 3% (i.e. nine times less than *T. vulgaris* or *T. alpestris*, the most common species). Even with a very large sample size as there is here, it was difficult to determine its habitat preference. The models showed that ponds must be deep enough (more than 70 cm) to allow conservation of *T. cristatus*. A high density of ponds (Joly *et al*., 2001) would certainly be beneficial but, as shown for other species (see also Denoël and Lehmann, 2006), maintaining a large number of ponds would not help conservation if the ponds do not offer suitable habitat. Specific surveys and longitudinal monitoring of this endangered species are necessary to plan for conservation and to stop the current decline. However, no such local action has been taken yet, except for the insufficient step of possibly designating some of the sites in Natura 2000 (Denoël, 2004a). More work is particularly needed at a fine-scale range to characterize the most valuable micro-habitats (see, for example, Oldham *et al*., 2000).

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As the other species were more abundant in the study area, it was possible to identify both pond and landscape features that are important for their persistence. As for *T. cristatus*, water bodies must be managed by removing excess organic matter and possibly re-digging them to retain enough water during the breeding period of newts. Although some limited financial help can be offered to farmers to maintain their ponds, the best way would be for the ponds to continue their role of watering cattle and providing water reserves. However, with a higher water volume due care should be taken to avoid the introduction of fish. If already present in ponds where they should not be, fish should be removed or the newts will largely decline (Denoël *et al*., 2005). To this end, it may be necessary to net or empty the ponds (Knapp and Matthews, 1998).

At the landscape scale, the present study strongly suggests that managing only the pond features is not enough because different species require different landscape features (*T. vulgaris*: meadows; *T. alpestris* and *T. helveticus*: forest), and because the spatial configuration of patches (i.e. forest proximity to ponds) influences newt distribution. Although *T. vulgaris* is particularly associated with open areas, *T. alpestris* and *T. helveticus* need some forest cover (20% and 40% on average) and *T. helveticus* requires a short distance to the forest (26 m on average). Given the scarcity of woodlands in the central part of Pays de Herve, conservation priority should be given to forest patches and to ponds close to forest. Finally, a key finding of our study is the remarkable difference in habitat requirements observed among species. Therefore, to conserve entire newt guilds it is imperative to maintain a variety of habitats, even if some of them are not necessary for each species. Pays de Herve is composed of a mosaic structure of large meadows, small forest patches and wetlands. All these elements should be maintained to permit the different species to survive since the four newt species differ in their ecological preferences.

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