ACTA OECOLOGICA 35 (2009) 53–59

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/actoec

Original article

Pond and landscape determinants of *Rana dalmatina* population sizes in a Romanian rural landscape

Tibor Hartel[a,*], *Szilárd Nemes*[b], *Dan Cogălniceanu*[c], *Kinga Öllerer*[d], *Cosmin Ioan Moga*[a], *David Lesbarrères*[e], *László Demeter*[f]

[a]*Mihai Eminescu Trust, Strada Cojocarilor nr. 10, 545400 Sighişoara, Romania*
[b]*University of Gothenburg, School of Mathematical Sciences, 41296 Göteborg, Sweden*
[c]*Ovidius University, Faculty of Natural Sciences, 900527 Constanţa, Romania*
[d]*Institute of Biology, Romanian Academy, 060031 Bucharest, Romania*
[e]*Biology Department, Laurentian University, Sudbury, Ontario P3E 3C6, Canada*
[f]*Sapientia EMTE, Department of Technical and Nature Sciences, 530104 Miercurea-Ciuc, Romania*

ARTICLE INFO

Article history:
Received 4 February 2008
Accepted 5 August 2008
Published online 14 September 2008

Keywords:
Rural landscapes
Rana dalmatina
Population sizes
Conservation
Romania

ABSTRACT

Amphibians are good indicators of human impact, declining steadily worldwide. We explored the relationships between the ponds and nearby landscape parameters and population size of the Agile Frog (*Rana dalmatina*), estimated from the number of egg masses, in a cultural landscape within the central section of Târnava Mare Basin, Romania. Forty-three permanent ponds were surveyed in a 2600 km^2 area. The average number of egg masses per pond was 211.13 (SD = 426.41). The egg mass number was significantly and positively related to the emergent aquatic macrophyte cover (its effect peaks at around 50%) and the green connecting corridors between the ponds and forests, and negatively related to the extent of nearby urban areas. The proximity of the forest (positive effect) and the presence of high traffic roads (negative effect) were highly correlated with green corridors and further eliminated from the model due to multicollinearity. Both these variables had significant effects when incorporated in univariate models and multivariate models without green corridors. Since a large part of our study area was currently declared as Natura 2000 site, there is an increased need for management proposals and conservation applications for biodiversity, including amphibians. *Rana dalmatina* is an important species for monitoring because it is common in the studied area and is suited for short surveys.

1. Introduction

Ecosystems are substantially altered by human activities through several interacting processes (Vitousek et al., 1997). However, the intensity of the human impact is not uniformly distributed. In many parts of Central and Eastern Europe land use is still traditional, resulting in highly diverse cultural/rural landscapes (Palang et al., 2006). Because this landscape is expected to further undergo drastic changes as result of infrastructural development, understanding what principal characteristics are important for various amphibian species is crucial. Pond breeding amphibians are important candidates as bioindicators of environmental health and for conservation because of their complex life cycles. Moreover, amphibians are

* *Corresponding author*. Tel.: +40 07 2085 6845.
E-mail address: asobeka@yahoo.com (T. Hartel).

1146-609X/$ – see front matter
doi:10.1016/j.actao.2008.08.002

in global decline (Stuart et al., 2004) due to various causes such are: habitat loss and fragmentation (Cushman, 2006), the introduction of non-indigenous species, especially fish (Kats and Ferrer, 2003), including invasive amphibians (Ficetola et al., 2007), emerging infectious diseases, climate change and increased UV-B radiation (Pounds et al., 2006). Because of their specific need for a high level of habitat complementation (aquatic and diverse terrestrial habitats inter-connected), amphibian species distribution and population sizes may not be accurately predicted using only habitat variables that describe the quality of a single habitat, most frequently the pond itself (the ''ponds as patches approach'', Marsh and Trenham, 2001). Since most pond breeding amphibians spend most of their post-metamorphic life in terrestrial habitats, except for the brief annual reproductive events, the quality of these habitats is extremely important for their persistence (Rittenhouse and Semlitsch, 2007). Thus, for a more complete description of the range of environmental factors that determine the distribution and abundance of amphibians, variables related both to pond and terrestrial areas should considered (i.e. Van Buskirk, 2005).

The Agile Frog (*Rana dalmatina*) is widely distributed in Europe (Grossenbacher, 1997). It is recorded in a number of landscape types; the most important being mixed deciduous forests up to 800 m altitude (Grossenbacher, 1997). The species is an explosive breeder, and within the study area is reproducing usually in the end of February – second part of April (Hartel, 2008). Breeding habitats include a wide range of aquatic habitats from temporary to permanent ponds and floodplains of temporary streams (Pavignano et al., 1990; Morand and Joly, 1995; Vignoli et al., 2007). In Romania, *Rana dalmatina* is listed as strictly protected according to the national legislation (Ministerial Order 1198/2007), requires a system of strict protection according to the European Council Directive 97/62/EC – Habitat Directive (Annex IV) and is endangered according to the Bern Convention (Annex II).

The aim of this paper is to evaluate the importance of relationships between the pond characteristics, the surrounding landscape parameters and the reproductive output of *Rana dalmatina* in a rural landscape from Romania. In particular, we hypothesize a positive relationship between the egg mass number and the pond characteristics such as the percentage of shallow water in the ponds, the emergent macrophyte vegetation cover, the total coverage of the other water bodies in the landscape, the extent of grasslands and pastures around the ponds. Moreover, we hypothesize a positive relationship with three variables related to the forest: the proximity of the pond to the forest, the forest cover and the connectivity with the forest. By contrast, we expect to observe negative associations between the egg mass number of *R. dalmatina* and the presence of predatory fish, the presence of high traffic roads, the extent of arable lands and urban areas within the landscape, and the water quality (acidity and conductivity).

2. Materials and methods

2.1. Study area and methods

The study area (center-point coordinates: N 46.22794; E 24.78053) is located in the middle section of the Târnava Mare Valley, Romania, and covers 2600 km^2. The area was described in detail in Hartel et al. (2007, 2008). The entire middle section of the Târnava Mare basin is representative for the Continental bioregion, consisting of a mixture of deciduous forests and grasslands that was maintained by the traditional land use from the Middle Ages to our days.

The localization of the ponds was described in detail in Hartel et al. (2008). The surveys were made between 2000 and 2007 in 43 permanent ponds, whereas in the case of one pond, the egg masses were counted beginning with 1997 (Hartel, 2008). We used egg mass counts as proxies of the population size, since they are a measure of the reproductive female population size. We assumed that each female lays only one egg mass per year. Since such surveys need to be carried out in a relatively short time (i.e. before the larvae hatch), sampling was performed each year from the end of February until the second half of April. Egg masses were easily detected as they are deposited in the shallow, warm areas of the pond. The permanent ponds were selected in a way to represent a random sample of the overall ponds available but also according to their accessibility (to make possible reliable counts of the egg masses). A single pond was surveyed for only 1 year (reproductive season), 17 ponds were surveyed for 2 years, 15 ponds for 3 years, three ponds for 4 years, two ponds for 5 years, four ponds for 6 years and one pond for 7 years. The average number of days per pond was 3.29 (minimum value = 3, SD = 1.05).

To better understand the relative importance of pond and landscape features in amphibian habitat use and population size, both pond and landscape variables have been used. In our approach, the landscape means the totality of patches (land cover types) that can be easily delimited and relatively easily visualized on maps and/or identified in the field. The land cover types are described at various distances (usually between 100 and 3000 m) around the ponds (potential breeding sites) in radius circles. These radiuses are considered based on the terrestrial migration distance of amphibians (e.g. Laan and Verboom, 1990; Joly et al., 2001; Houlahan and Findlay, 2003).

We considered six aquatic habitat (pond) and nine landscape variables for each sampled pond. The aquatic variables were: the pond area (m^2), the percentage of emergent aquatic vegetation cover (macrophytes: e.g. *Phragmites* sp. and *Typha* sp.), the percentage of shallow water (<50 cm depth), the presence/absence of non-predatory and predatory fish (see their description in Hartel et al., 2007, 2008), the water acidity (pH) and the water conductivity (μS/cm). Landscape variables were recorded within 800 m radius around individual ponds. We chose this distance because it encompasses the maximum movement distance recorded in *R. dalmatina* (Smith Alex and Green, 2005). These variables were: elevation (m), distance of pond from forest (m), presence/absence of green connecting corridors, forest cover in the landscape (%), pastures and grasslands cover in the landscape (%), arable land cover (%), urban area cover (%), wetland cover (%) and the presence/absence of high traffic roads (traffic intensity of up to 300 cars/h at night; Hartel et al., 2008). We defined as green corridors the areas (vegetation stripes, small springs) situated between ponds and forests that assumingly had more favorable conditions for the movement of *R. dalmatina* as opposed to bare arable land, roads, and urbanized areas. Land use composition around the ponds was analyzed using the GIS software Manifold 7x, based on data from the CORINE Land Cover map (European Environmental Agency, 2006) occasionally corrected by our ground estimations (Hartel et al., 2008).

2.2. Statistical procedures

Because of the highly significant correlation between the minimum, maximum and average number of egg masses recorded in the individual ponds (r varying from 0.92 to 0.99) we used the maximum number of counted egg masses in the statistical analysis. When ordinary linear regression cannot be used as an exploratory tool, Generalized Linear Models (GLM) can be used to transform the explanatory model to a linear scale. In the case of count data (positive integers) following a Poisson distribution, Poisson GLM can be used. However, our dataset violates the characteristic structural relationship between mean and variance thus Negative Binomial GLM was used to accommodate the overdispersed data.

A backward variable selection strategy was adopted based on Akaike Information Criterion. A full model with all covariates was build and then we tested how the removal of each parameter would influence the model. We also tested whether there is evidence against the removal of variables by Likelihood Ratio Test. To assess the effect of the final covariates on the removed ones, the final multivariate model was extended by adding one removed covariate and fitting a new multivariate model. The parameter estimates, regression coefficients and associated statistics of dispersion were then compared with the parameter estimates of the univariate models. Genuine changes in magnitude or a change in sign indicate strong effect of the final variables on the removed ones, presumably due to multicollinearity. All statistical analyses were carried out using R 2.61 (R Development Core Team, 2007) following Long (1997), and Faraway (2006).

3. Results

Rana dalmatina was present in 79.06% of the studied ponds. The average number of egg masses was 211.13 (SD = 426.41) and the median was 35 (minimum: 0, maximum: 2500, lower quartile = 4, upper quartile = 256). There was no correlation between the maximum number of egg masses recorded and the number of years in which each pond was surveyed ($r = -0.003$, $P > 0.05$).

Three predictor variables (urban area cover, green corridors, and macrophyte cover) influenced significantly the variability in the *R. dalmatina* egg masses. These three predictors had genuine predictive power (LRT $\chi^2 = 41.26$, df = 2, $P < 0.0001$) and their predictive capacity did not differ from the model incorporating all considered explanatory variables (LRT $\chi^2 = 15.43$, df = 10, $P = 0.11$). Removal of further explanatory variables reduced significantly the goodness of fit of the estimated model (Table 1).

Table 1 – Influence on residual deviance and AIC of the removal of further variables from the whole model (see Section 2). Likelihood Ratio Test against the removal is provided

	df	Deviance	AIC	LRT χ^2	P
No removal		46.90	406.19		
Urban area cover	1	60.89	418.18	13.99	<0.0001
Macrophyte cover	1	80.86	438.16	33.97	<0.0001
Green corridor	1	52.99	410.28	6.09	<0.0001
Quadratic effect of macrophyte	1	69.69	426.98	22.79	<0.0001

The proportion of urban areas was associated with a significant decrease in the number of egg masses (with an urban coverage of 40% or more, Fig. 1) while the presence of green corridors led to an increase (Table 2). The third significant predictor was the macrophyte cover which had a significant quadratic effect. The addition of the quadratic term genuinely improved the models goodness of fit ($\Delta_{AIC} = -20.79$). Thus the number of egg masses increased with increasing macrophyte cover until a threshold was reached (roughly a coverage of 50%), then its number decreased (Fig. 1). Based on changes in residual deviance and AIC values, macrophyte cover had the largest influence on the egg mass number, followed by the negative impact of urbanized areas then the positive effect of green corridors (Table 1).

The extended multivariate model and comparisons with the univariate models evidenced two noteworthy differences. Univariate model fitting showed significant negative effect for both distance from the forest (distance from the forest: $\beta \pm$ SE: -0.0023 ± 0.00079, $Z = -2.89$, $P = 0.004$) and roads ($\beta \pm$ SE: -2.08 ± 0.53, $Z = -3.86$, $P = 0.0001$). In the extended multivariate models the coefficient estimates of both predictors show substantial change. The effect of distance from the forest became positive and non-significant ($\beta \pm$ SE: 0.00092 ± 0.00094, $Z = 0.97$, $P = 0.33$). Similarly, the relationship between the egg mass number and roads becomes positive and non-significant ($\beta \pm$ 1SE: 0.94 ± 0.67, $Z = 1.40$, $P = 0.16$).

Thorough examinations indicate that effects of pond distance from forest and presence of road were masked by the effect of green corridors. Distance from the forest is highly and negatively correlated with green corridors ($r = -0.794$, $t = -8.24$, df = 39, $P < 0.0001$) while the parameter estimates from the extended multivariate model are positively correlated ($r_\beta = 0.78$). Again, the pattern is similar for the roads: roads and green corridors were highly and negatively correlated ($r = -0.797$, $t = -8.24$, df = 39, $P < 0.0001$) while their regression coefficients from the extended multivariate model are positively correlated ($r_\beta = 0.78$). No significant relationship was found between the number of egg masses and the other variables measured.

4. Discussion

The most important pond and landscape elements that best predict the distribution of *R. dalmatina* were identified using multivariate statistical tools. This allows the proposal of specific management measures in order to efficiently protect amphibian populations (see for example Vos and Chardon, 1998; Houlahan and Findlay, 2003; Van Buskirk, 2005; Eigenbrod et al., 2008).

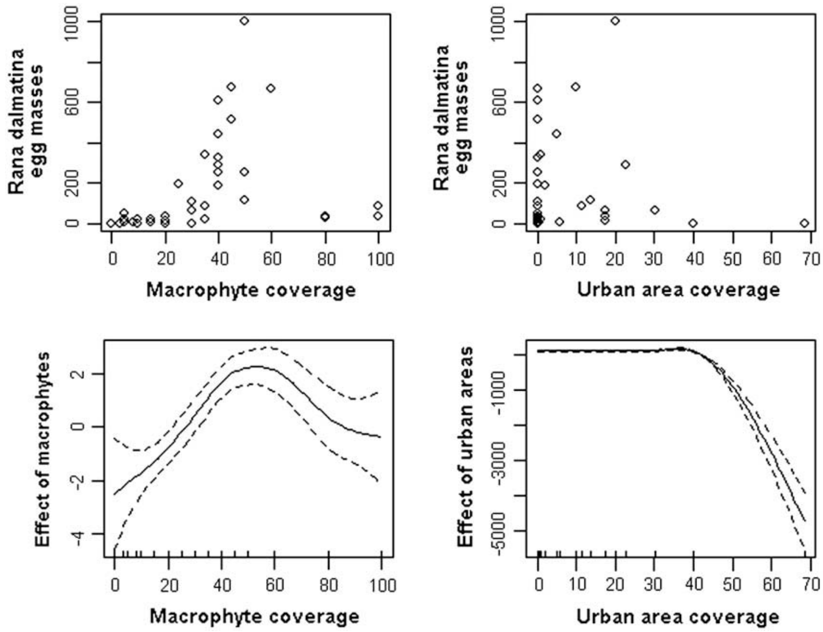

Fig. 1 – Relationship between the distribution of *Rana dalmatina* egg masses and (a) the variation of macrophyte cover, (b) the urban area coverage (upper row) and the smoothed effect of the two covariates on the egg mass number (lower row).

The constructed regression models showed that four landscape related variables (the extent of urban areas, the pond connectivity with the forest, the distance of the ponds from the forest and the presence of the high traffic roads) and one pond variable (the emergent aquatic vegetation cover) influence the egg mass number. Information-theoretic model selection approach based on Akaike Information Criterion demonstrated that the effect of macrophyte cover is stronger than that of the landscape related variables. Since a large area was currently declared as Natura 2000 site, there is an increased need for management proposals and conservation applications for biodiversity, including amphibians. Identifying the main habitat and landscape predictors of the egg mass counts offer practical solutions in this direction.

4.1. *The importance of pond variables*

A recent study carried out on a larger sample of permanent ponds (85) in this area (Hartel et al., 2007) showed the importance of the reed coverage for the amphibian communities and the pond occupancy of six species, including *Rana dalmatina*.

Table 2 – Estimates of the Negative Binomial regression on the effect of predictors for the number of egg masses

	β	SE (β)	Z	Pr(>|z|)
(Intercept)	0.575	0.557	1.032	0.3022
Urban area cover	−6.759	1.615	−4.185	<0.0001
Macrophyte cover	0.156	0.024	6.346	<0.0001
Green corridor	1.244	0.5171	2.404	0.0162
Quadratic effect of macrophyte	−0.001	0.0002	−5.295	<0.0001

Associations between the spawning site selection by *R. dalmatina* and the aquatic vegetation cover were also demonstrated by Pavignano et al. (1990), Kecskés and Puky (1992) and Ficetola et al. (2006). Vegetation cover may have a series of benefits for amphibians. Emergent vegetation may limit the impact of predators. The developmental stages most exposed to predation in amphibians are the egg and larval stages, the later being the most documented one as well. To coexist with predators, special adaptations are required like decreasing activity, behavioral avoidance using chemical cues, toxic compounds and phenotypic plasticity (see for example Semlitsch and Reyer, 1992; Van Buskirk, 2001; Teplitsky et al., 2003). All these adaptations are efficient in the context of habitat structural complexity (Tarr and Babbitt, 2002). The lack of relationships between the presence/absence of fish (both predatory and non-predatory) and the egg mass number of *R. dalmatina* may be caused by the large reed coverage and the behavioral adaptations of larvae (Hartel et al., 2007). The presence of habitat refugia secured by vegetation increases the survival of *R. dalmatina* tadpoles when the fish *Pseudorasbora parva* (a fish species that is abundant in these ponds (Hartel et al., 2007)) is present (Teplitsky et al., 2003). Moreover, reed may represent support for the egg masses (Kecskés and Puky, 1992; Lesbarrères and Lodé, 2002; Ficetola et al., 2006) and may provide surface for algal development (that constitutes food for the tadpoles). Our study showed that the effect of the macrophyte cover is positive until a threshold (around 50% in our study) after which the macrophyte cover has a negative effect on the number of egg masses. A long term study carried out in a *R. dalmatina* population from the Tarnava Mare basin (Hartel, 2008) suggests that when available, *R. dalmatina* females select parts of the breeding pond where the vegetation is in an early succesional stage. In *R. lessonae* populations, it was shown that the vegetational overgrowing of the ponds may cause deterministic extinctions (Sjögren-Gulve, 1991). Additionally, Oldham et al. (2000) observed that *T. cristatus* has the highest pond occupancy in ponds with emergent vegetation cover between 25 and 50% and submergent vegetation between 50 and 75%. Although the space available for newt activity was suggested as a limiting factor (Oldham et al., 2000), we suspect that the changes in the ecological conditions linked with the increase of the reed coverage (temperature, light conditions and productivity) may also affect the selection of ponds suitable for spawning. As the reed cover may increase in time through natural succession, management interventions should be done to allow the maintenance of the reed cover that allows breeding conditions for *R. dalmatina*.

Barton and Rafinski (2006) found that the eggs of *R. dalmatina* degenerated at pH of around 4.3. In our study area the pH values measured in the ponds are well beyond this value (mean 7.56, min–max: 6.02–8.94) and no relationship was observed between the amphibian species richness and the water acidity and conductivity in this area (Hartel et al., 2006), showing that there is no acidification threat for amphibians in this area. Similarly, Loman and Lardner (2006) showed in a field experiment that the acidity and conductivity were not responsible for the absence of *R. temporaria* and *R. arvalis* from the intensively used farmlands, although the ponds situated in these landscapes had higher acidity and conductivity. Finally, we failed to find a relationship between the percentage of shallow water and the number of egg masses in this area, most likely due the wide extent of the shallow zones within the ponds.

4.2. *The importance of landscape variables*

The number of egg masses in *R. dalmatina* was positively associated with two variables that are related to the availability of a forest patch in the landscape: the connectivity and proximity of the forest. As the distances from forest increase (as a result of forest clearings for agricultural and urban expansion), and new roads are built, there is an increasing need for the presence of green corridors to counteract this negative effect. The distance of the breeding ponds from the forest is particularly important for *R. dalmatina*. In a study conducted by Ponséro and Joly (1998) on this species, the majority of egg masses were found in ponds situated within 50–100 m distance from forest. According to Lesbarrères and Lodé (2002) the size of both the egg masses and the number of eggs of *R. dalmatina* were larger in the forested ponds than in ponds situated in open areas. The type of the deciduous forests is also important for *R. dalmatina*: the body condition index of the Agile Frogs was higher in the humid forests (*Stellario-Carpinetum*) than in the dryer forests (*Galio odorati-Fagetum*) (Stümpel and Grosse, 2005). The importance of the forested areas and/or variables related to forests for amphibians is highlighted by many studies on different species that used a similar approach to ours. European examples are *B. bufo* (Scribner et al., 2001), *R. temporaria* (Van Buskirk, 2005), newts species from *Triturus* genera (Joly et al., 2001; Van Buskirk, 2005). Studies from North America that used multiple species approaches (e.g. Hecnar and M'Closkey, 1998; Guerry and Hunter, 2002; Houlahan and Findlay, 2003) also demonstrated the importance of the forest proximity and/or coverage for different species at different spatial scales.

Estimates of the Negative Binomial regression showed a negative relationship between the egg mass number and the urbanized areas. The univariate analysis evidenced the negative association between the egg mass number and high traffic roads. Both may cause habitat loss and may have isolation effects on the critical habitats and the populations. Pellet et al. (2004) showed that the urban areas affect the pond use of the European Tree Frog (*Hyla arborea*) in a distance of up to 1 km. In our study, the urban area effect is negative after a rough coverage of 40%. The traditionally managed human settlements in the cultural landscapes may not represent habitat destruction for amphibians in this area. Amphibians may use different landscape elements from the villages as summering (for example the small orchards nearby the houses) and wintering (the cellars). The negative impact of roads on amphibian populations is demonstrated by an increasing number of studies. Roads may increase the likelihood of inbreeding, local extinction and lead to high level of population differentiation (as demonstrated for *R. dalmatina* by Lesbarrères et al., 2003, 2006), increase mortality during seasonal movements (Vos and Chardon, 1998; Hels and Buchwald, 2001). The effect of road traffic may be at least as strong as the effect of deforestation (Eigenbrod et al., 2008) and habitat split (Becker et al., 2007). A recent survey carried out on a 83 km long road transect in the area of our study estimated up to 1400 *R. dalmatina* road-kills in 2 weeks during the breeding season along high traffic roads (Hartel unpublished results).

We did not find any significant effect of the amount of arable lands and the grassland/pasture cover in the landscape on the number of egg masses. When intensively applied, both land use practices may reduce the terrestrial habitat available for frogs and disrupt the connectivity between critical habitats (feeding, breeding and hibernating; Joly et al., 2001; Rubbo and Kiesecker, 2005). In our study area both land use types are traditional. However, *R. dalmatina* uses open habitats mostly during seasonal migrations (in spring and autumn) in this area and the forest during the summer months making the identification of potential effects of these land uses (arable lands and grasslands) more difficult.

Similarly, we expected a positive relationship between the water body coverage in the landscape around the studied ponds and the number of egg masses (Laan and Verboom, 1990; Houlahan and Findlay, 2003; Ficetola and De Bernardi, 2004) but failed to find such relationship. This may be explained by the fact that the water bodies around ponds are represented by running waters in almost all cases (springs and the Târnava Mare river). The small flooded areas along these streams may be used by Agile Frogs (excepting the river), but are not stable habitats and do not allow the formation of larger populations (always less than 10 egg masses per site, Hartel, pers. obs.). Furthermore, in the case of ponds from Vanatori and Albesti regions, the pond availability is large but the lack of terrestrial habitats may limit the size of the population.

5. Conclusions and implications for conservation management

The number of *R. dalmatina* egg masses in this landscape can be predicted by the emergent aquatic macrophyte vegetation cover but not in a linear way: the positive effect of macrophytes peaks at around 50% and after this percentual coverage, its effect on the egg masses is negative. As many ponds become private properties and the fish introduction are becoming more and more popular (Hartel et al., 2007), the necessity for the aquatic vegetation as buffer against fish predation is enhanced.

The critical landscape elements that should be maintained to allow the persistence of high *R. dalmatina* population numbers are the green corridors and the proximity of the forest. These may counteract the effect of habitat loss caused by roads and settlements. As amphibians may disperse at considerable distances and their population sustainability depends both on the dispersal success and colonization process (Smith Alex and Green, 2005) conservation measures should go beyond the 800 m radius considered in this study. Further studies should identify these landscape elements on maps in order to make scientific results available to landowners and involve landscape planners in the effective management and conservation of amphibians in this area. We suggest that *R. dalmatina* may be an important target species for long term monitoring in the studied area because it is common, it is easily to be identified in the field and a long term database is already available for one population of this species (11 years, Hartel, 2008).

Acknowledgements

The authors would like to thank the *Declining Amphibian Populations Task Force*, the *Swedish Biodiversity Center* and the *Mihai Eminescu Trust* for their financial support as well as comments from two anonymous reviewers that greatly improved this manuscript.

REFERENCES

Barton, K., Rafinski, J., 2006. Co-occurrence of Agile Frog (*Rana dalmatina* Fitz. in Bonaparte) with Common Frog (*Rana temporaria* L.) in breeding sites in southeastern Poland. Polish J. Ecol 54, 151–157.

Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F., Prado, P.I., 2007. Habitat split and the global decline of amphibians. Science 318, 1775–1777.

Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biol. Conserv 128, 231–240.

Eigenbrod, F., Hecnar, S.J., Fahrig, L., 2008. The relative effects of road traffic and forest cover on anuran populations. Biol. Conserv 141, 35–46.

Faraway, J.L., 2006. Extending Linear Models with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models. Chapman & Hall/CRC, Boca Raton, FL.

Ficetola, G.F., De Bernardi, F., 2004. Amphibians in a human dominated landscape: the community structure is related to habitat features and isolation. Biol. Conserv 119, 219–230.

Ficetola, G.F., Valota, M., de Bernardi, F., 2006. Temporal variability of spawning site selection in the frog *Rana dalmatina*: consequences for habitat management. Anim. Biodiv. Conserv 29, 157–163.

Ficetola, G.F., Thuiller, W., Miaud, C., 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. Div. Distrib 13, 476–485.

Grossenbacher, K., 1997. *Rana dalmatina,* Bonaparte 1840. In: Atlas of Amphibians and Reptiles in Europe. Societas Europaea Herpetologica & Museum National d'Histoire Naturelle (IEGB/SPN), Paris, p. 494.

Guerry, A.D., Hunter, M.L., 2002. Amphibian distribution in a landscape of forest and agriculture: an examination of landscape composition and configuration. Conserv. Biol. 16, 745–754.

Hartel, T., 2008. Within pond variation of the egg deposition site in *Rana dalmatina*. Biologia 3, 439–443.

Hartel, T., Demeter, L., Cogălniceanu, D., Tulbure, M., 2006. The influence of habitat characteristics on amphibian species richness in two river basins of Romania. In: Vences, M., Köhler, J., Ziegler, T., Böhme, W. (Eds.), Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica, Bonn, pp. 47–50.

Hartel, T., Nemes, Sz., Cogălniceanu, D., Öllerer, K., Schweiger, O., Moga, C.I., Demeter, L., 2007. The effect of fish and habitat complexity on amphibians. Hydrobiologia 583, 173–182.

Hartel, T., Nemes, Sz., Demeter, L., Öllerer, K., 2008. Pond and landscape characteristics: which are more important for the common toad? A case study from central Romania. Appl. Herp 5, 1–12.

Hecnar, S.J., M'Closkey, R.T., 1998. Species richness patterns of amphibians in southwestern Ontario ponds. J. Biogeogr 25, 763–772.

Hels, T., Buchwald, E., 2001. The effect of road kills on amphibian populations. Biol. Conserv 99, 331–340.

Houlahan, J.E., Findlay, C.S., 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. Can. J. Fish Aquat. Sci. 60, 1078–1094.

Joly, P., Miaud, C., Lehmann, A., Grolet, O., 2001. Habitat matrix effect on pond occupancy in newts. Conserv. Biol. 15, 239–248.

Kats, L.B., Ferrer, R.P., 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Div. Distrib 9, 99–110.

Kecskés, F., Puky, M., 1992. Spawning preference of the agile frog, *Rana dalmatina*. In: Korsós, Z., Kiss, I. (Eds.), Proc. Sixth. Ord. Met, 1991. SHE, Budapest, pp. 251–254.

Laan, R., Verboom, B., 1990. Effects of pool size and isolation on amphibian communities. Biol. Conserv 54, 251–262.

Lesbarrères, D., Lodé, T., 2002. Influence de facteurs environnementaux sur la reproduction de *Rana dalmatina* (Anura, Ranidae): implications pour sa conservation. Bull. Soc. Herp. Fr 104, 62–71.

Lesbarrères, D., Pagano, A., Lodé, T., 2003. Inbreeding and road effect zone in a Ranidae: the case of agile frog *Rana dalmatina* Bonaparte 1840. C.R. Biol. 326, 68–72.

Lesbarrères, D., Primmer, C.R., Lodé, T., Merilä, J., 2006. The effect of 20 years of highway presence on the genetic structure of *Rana dalmatina* populations. Ecoscience 13, 531–538.

Loman, J., Lardner, B., 2006. Does pond quality limit frogs *Rana arvalis* and *Rana temporaria* in agricultural landscapes? A field experiment. J. Appl. Ecol 43, 690–700.

Long, J.S., 1997. Regression Models for Categorical and Limited Dependent Variables. Sage Series for Advanced Quantitative Techniques. Sage Publications, Thousand Oaks, CA.

Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. Conserv. Biol. 15, 40–49.

Morand, A., Joly, P., 1995. Habitat variability and space utilization by the amphibian communities of the French Upper-Rhone floodplain. Hydrobiologia 300/301, 249–257.

Oldham, R.S., Keeble, J., Swan, M.J.S., Jeffcote, M., 2000. Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). Herpet. J. 10, 143–155.

Palang, H., Printsmann, A., GyuróÉ, K., Urbanc, M., Skowronek, E., Woloszyn, W., 2006. The forgotten landscapes of Central and Eastern Europe. Landsc. Ecol 21, 347–357.

Pavignano, I., Giacoma, C., Castellano, S., 1990. A multivariate analysis of amphibian habitat determinants in north western Italy. Amphibia-Reptilia 11, 311–324.
Pellet, J., Guisan, A., Perrin, N., 2004. A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. Conserv. Biol. 18, 1599–1606.
Ponséro, A., Joly, P., 1998. Clutch size, egg survival and migration distance in the agile frog (*Rana dalmatina*) in a floodplain. Arch. Hydrobiol. 142, 343–352.
Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P., Foster, L., La Marca, P.N.E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J., Young, B.E., 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439, 161–167.
R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
Rittenhouse, T.A.G., Semlitsch, R.D., 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands 27, 153–161.
Rubbo, M.J., Kiesecker, J.M., 2005. Amphibian breeding distribution in an urbanized landscape. Conserv. Biol. 19, 504–511.
Scribner, K.T., Arntzen, J.W., Burke, T., Cruddace, N., Oldham, R.S., 2001. Environmental correlates of toad abundance and population genetic diversity. Biol. Conserv 98, 201–210.
Semlitsch, R.D., Reyer, H.U., 1992. Modification of anti-predator behavior in tadpoles by environmental conditioning. J. Anim. Ecol 61, 353–360.
Sjögren-Gulve, P., 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biol. J. Linn. Soc. 42, 135–147.
Smith Alex, M., Green, D.M., 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28, 110–128.
Stuart, S.N., Chanson, I.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fishman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 3, 1783–1785.
Stümpel, N., Grosse, W.-R., 2005. Phenology, activity and growth of agile frogs (*Rana dalmatina*) in different summer habitats of southeast Lower Saxony. Zeit. Feldherpetol 12, 71–99.
Tarr, T.L., Babbitt, K.J., 2002. Effects of habitat complexity and predator identity on predation of *Rana clamitans* larvae. Amphibia-Reptilia 23, 12–20.
Teplitsky, C., Plénet, S., Joly, P., 2003. Tadpoles' response to risk of fish introduction. Oecologia 134, 270–277.
Van Buskirk, J., 2001. Specific induced responses to different predator species in anuran larvae. J. Evol. Biol. 14, 482–489.
Van Buskirk, J., 2005. Local and landscape influence on amphibian occurrence and abundance. Ecology 86, 1936–1947.
Vignoli, L., Bologna, M.A., Luiselli, L., 2007. Seasonal patterns of activity and community structure in an amphibian assemblage at a pond network with variable hydrology. Acta Oecol 31, 185–192.
Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.
Vos, C.C., Chardon, J.P., 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog, *Rana arvalis*. J. Appl. Ecol 35, 44–56.