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Spatial and temporal variability of aquatic habitat use by amphibians in a hydrologically modified landscape

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SUMMARY

1. Habitat loss is a major driver of biodiversity decline worldwide. Temporary waterbodies are especially vulnerable because they are sensitive both to human impact and to climatic variations. Pond-breeding amphibians are often dependent on temporary waterbodies for their reproduction, and hence are sensitive to loss of temporary ponds.

2. Here we present the results of a 5-year study regarding the use of temporary aquatic habitats by amphibians in a hydrologically modified area of Eastern Europe (Romania). The annual number of aquatic habitats varied between 30 and ~120. Each aquatic habitat was characterised by a number of variables such as: ‘type’ (pond, drainage ditch and archaeological ditch), ‘hydroperiod’ (number of weeks the ponds were filled in a given year), ‘depth’ (cm), ‘area’ (m²) and the density of predatory insects (‘predation’). The turnover rate for each amphibian species for each wetland was calculated based on the pond occupancy.

3. Eight amphibian species were recorded from the aquatic habitats. Hydroperiod was the most important variable, positively influencing wetland use by amphibians and their reproductive success. Most species preferred drainage ditches for reproduction, and the reproductive success was highest in this habitat type every year. For most of the species, the local extinction rate was higher than the colonisation rate in the first 4 years, but the situation reversed in the last year of the study when wetland use by amphibians sharply increased because of high rainfall.

4. This study confirms the importance for amphibians of maintaining and managing aquatic habitat diversity at small spatial scales. Man-made aquatic habitats such as drainage ditches may be important habitats for amphibians, and this should be considered in restoration activities.

Keywords: amphibian, aquatic habitat use, colonisation, extinction, patchy population

Introduction

The sharp decline in biodiversity caused by habitat loss (e.g. Fahrig, 2003) calls for increasing efforts to manage habitats to keep them suitable for wildlife (Akçakaya & Sjögren-Gulve, 2000). Conservation

managers need to understand the spatio-temporal variation of habitat availability and use for the focal organisms (e.g. Runge, Runge & Nikols, 2006). The proper management of habitats should contribute to the sustainability of local populations. However, delineating natural populations based on habitat extent is often difficult (Berryman, 2002; Camus & Lima, 2002). At one extreme, organisms may be linked to clearly delimitable habitat patches, each patch supporting independent demographic units (i.e.

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populations). The population size and persistence may be positively related to the size of the habitat patch, and at the regional (metapopulation) level, the persistence of organisms will depend on colonisation–extinction events of individual habitat patches (Hanski, 2001). When larger habitat patches contribute more to regional persistence of species than small habitat patches (Pellet *et al.*, 2007), larger patches should be prioritised for conservation. In other cases, organisms are ‘distributed over a patchy and/or spatio-temporally variable habitat, but in which high rates of dispersal effectively unite the patches into a single demographic entity’ (Harrison, 1991). Such population structures are referred to as ‘patchy populations’ (Harrison, 1991). Patchy populations occupy environments where the source-sink character of the area is complex (Thomas & Kunin, 1999; Runge *et al.*, 2006). In such cases, conservation strategies should consider the maintenance of clusters of habitats rather than single large patches to maintain viable local populations.

Temperate pond-breeding amphibians are an excellent target group for studying organism occurrence in relation to habitat quality. First, they depend on both aquatic (for reproduction) and terrestrial (for feeding, overwintering, migration, dispersal) habitats (Hecnar & M’Closkey, 1996; Gibbons, 2003; Pellet *et al.*, 2007). Second, amphibians show both patchy and metapopulation structure depending on the aquatic habitat density, character (temporary or permanent), degree of clustering and the spatial scale on which they are distributed. If the aquatic habitats are clustered and close enough to allow regular movements of adults between them, the ‘pond populations’ may lose their demographic independence and a patchy population structure is likely (Pechmann *et al.*, 1991; Sinsch, 1992; Petranka, Smith & Scott, 2004; Jehle, Burke & Arntzen, 2005; Werner *et al.*, 2007a). Adult amphibians may actively choose breeding sites to avoid larval mortality through desiccation (Wellborn, Skelly & Werner, 1996), competition (Petranka, & Holbrook, 2006), predation (Hopey & Petranka, 1994; but see Laurilä & Aho, 1997) and parasitism (Kiesecker & Skelly, 2000) or may be attracted to ponds by the presence of conspecific individuals (Rudolf & Rödel, 2005). In such population systems, the relative contribution of individual ponds to the overall population size can vary in time and space (Rudolf & Rödel, 2005). At wider spatial scales, amphibian persistence can be governed by metapopu-

lation-related processes such as extinction and (re)colonisation of aquatic habitats (Gill, 1978; Sjögren-Gulve, 1991; Pellet *et al.*, 2007). Finally, amphibian populations are globally declining. Although several causes of decline have been documented (Stuart *et al.*, 2004), those related to habitat loss are the most obvious and reversible (Cushman, 2006). Local and regional amphibian decline has been related to the loss of breeding habitats or the deterioration of their quality (Curado, Hartel & Arntzen, 2011).

In this study, we present the spatio-temporal variability of breeding habitat use of an amphibian community with a patchy population structure. The overall goal was to understand the relative importance of different aquatic habitat types for the persistence of amphibians. More specifically we address: (i) the variability of breeding habitat use and reproductive success according to aquatic habitat type and year, (ii) the colonisation–extinction rate of amphibian species in individual habitats and (iii) the breeding habitat parameters governing habitat occupancy and species richness.

Methods

Study area description and data collection

The studied area covers 133 ha and is situated in the middle section of the Târnava Mare Valley (central Romania), near the town of Sighișoara, at about 515 m elevation. The area is a wood pasture reserve (a pasture scattered with old trees such as *Quercus robur* and *Q. petraea*) and is surrounded by deciduous forest. The native vegetation cover (grassland and forest) is not fragmented by buildings or roads, and low-intensity grazing is the only management intervention applied to the area.

The climate of the area is continental. The amount of precipitation in January–June (the critical period for the formation and maintenance of temporary ponds as habitats for amphibians) was ~301 mm in 2006, ~237 mm in 2007, ~356 mm in 2008, ~264 mm in 2009 and ~437 mm in 2010 (source: Sibiu Meteorological Station).

The aquatic habitats in this area are small temporary, stagnant water bodies, formed and maintained by precipitation (the only source of water in the studied area). Their annual number varied between 30 and ~120. Generally, the distance between the two

closest waterbodies was <100 m and they were situated at up to 150 m from the forest margin. Aquatic habitats were grouped into three types: (i) 'ponds' that have a semi-natural origin, (ii) 'drainage ditches' that were created in the 1980s and (iii) 'archaeological ditches' created during archaeological research in 2001–02. The 'ponds' had the shortest hydroperiod, whereas the 'drainage ditches' were the most constant and the 'archaeological ditches' were intermediate (Table 1). The number of aquatic habitats in the surrounding forest was up to 30, and all had an ephemeral character. Occasional reproduction of *Bombina variegata* (Linnaeus, 1758), *Rana dalmatina* (Bonaparte, 1840) and *Rana temporaria* (Linnaeus, 1758) was observed in these habitats. These forest ponds were not monitored every year.

Amphibian and habitat data were collected in 2006–10. Surveys started with pond formation after snow and ice-melt (February) and were carried out weekly until the end of September. As the explosive breeder (*sensu* Wells, 1977) amphibian species (e.g. *Bufo bufo* (Linnaeus, 1758), *R. dalmatina* and *R. temporaria*) reproduce in March–April, all ponds were surveyed at least three times in this period to identify breeding adults. Surveys carried out in May–September aimed to detect prolonged breeders (*Hyla arborea* (Linnaeus, 1758), *B. variegata*, *Triturus cristatus* (Laurentus, 1768) and *Lissotriton vulgaris* (Linnaeus, 1758)), amphibian larvae and metamorphosis (as a measure of reproductive success) and to record the hydroperiod of wetlands. In the case of small waterbodies (up to ~30 m² surface area and up to 20 cm depth), all amphibian life stages could be easily identified by a visual search. In larger and deeper waterbodies, up to ~20% of the wetland surface was dipnetted. Dipnetting was complemented by torch counts and call surveys. For each of the three

aquatic habitat types, we recorded the presence or absence of adults, eggs and metamorphs.

Explanatory variables

When selecting the aquatic habitat variables, we assumed that the studied populations had a 'patchy population' character (*sensu* Harrison, 1991; Driscoll, 2007). This assumption was based on the proximity of the aquatic habitats (generally within ~100 m), this being within the migration and dispersal distance of those amphibian species recorded in this area (e.g. several hundreds of metres; Smith & Green, 2005) and the high spatio-temporal variability of the aquatic habitats (at least with respect to their hydroperiod, Table 1). Moreover, the terrestrial habitats were represented by continuous native vegetation cover, not fragmented by roads or built-up areas. Preliminary analyses showed that the forest distance from the aquatic habitats had no influence on amphibian breeding habitat use (Hartel, 2008). In these conditions, we assume that the spatio-temporal variability of breeding habitat use by different species is primarily constrained by features of the aquatic habitats.

Each aquatic habitat was described with the following variables: 'type' ('pond', 'drainage ditch' or 'archaeological ditch', see above), 'area' (m² in early spring after snow melt), 'depth' (maximum depth in cm after snow melt) and 'hydroperiod' (the number of weeks the wetlands contained water beginning with their spring formation). The abundance category of invertebrate predators ('predators' - larvae of *Odonata* and *Coleoptera* in the breeding period of amphibians) was recorded as '0' if no insect larva was found, '1' when the number of larvae were up to 10, '2' if the number of larvae was up to 20 and '3' if the number of insect larvae was up to 30. Other variables, such as water pH and conductivity, and the vegetation cover, were not measured in all years, but preliminary exploratory analysis showed that these parameters had no influence on amphibian habitat use (Hartel, 2008). We are therefore confident that the variables we recorded were those most likely to influence amphibian breeding habitat use in this system.

Data analysis

We calculated the annual extinction and colonisation rate for each amphibian species based on the

Table 1 The hydroperiod (number of weeks the aquatic habitats contained water) of the aquatic habitats in 2006–10

	Ponds	Archaeological ditches	Drainage ditches
2006	6.12 (4.29)	8.86 (4.85)	11.30 (4.86)
2007	3.35 (2.27)	4.11 (1.91)	5.65 (2.43)
2008	3.24 (3.98)	4.24 (6.19)	13.18 (7.54)
2009	Only three ponds formed	2.36 (3.32)	11.90 (8.27)
2010	10.96 (6.32)	17.47 (8.85)	26.54 (11.12)

Numbers in brackets represent the standard deviation.

presence or absence of adults, eggs and larval stages (the presence of these life stages being highly correlated). The extinction rate was calculated as the number of aquatic habitats where losses were registered (i.e. 'local extinctions') in a given year divided by the total number of aquatic habitats occupied in the previous year. Similarly, the colonisation rate was calculated by dividing the number of aquatic habitats with gains (i.e. colonisations) by the total number of aquatic habitats occupied in the previous year (Hecnar & M'Closkey, 1997a; Hartel & Öllerer, 2009). The overall rate of extinction and colonisation for each species was calculated as the sum of yearly extinction and colonisation rates divided by the overall number of years (i.e. four). For this analysis, we only considered aquatic habitats which contained water and excluded those that dried out in a particular year.

Linear regression was used to explore the relationship between the maximum movement distance from breeding ponds (in metres, log transformed) of individual species reported in the literature (from Smith & Green, 2005; Hartel, 2008 and unpublished data of TH) and the number of aquatic habitats colonised by adults every year. A positive relationship would indicate that species able to move (disperse) over longer distances will be present in more habitats (given that the isolation by distance is not a limiting factor in the studied system). A non-significant relationship would indicate that the quality of the aquatic habitats may be a factor limiting their use (Hartel & Öllerer, 2009). The Bray–Curtis association measure was used to calculate the dissimilarity between species based on their presence or absence at ponds. The unweighted pair group-mean-average (UPGMA) fusion algorithm was used to produce the dendrogram. We used the information-theoretic model selection approach to identify appropriate models best supported by the data (Burnham & Anderson, 2002). All continuous variables were z-transformed (standardised to an average of zero and a standard deviation of one) to increase comparability of the variables effects. A total of 63 models were designed. The first six candidate models included a single factor each: 'year' (Y), 'type' (T), 'predators' (P), 'depth' (D), 'area' (Z) and 'hydroperiod' (H). We also considered models that included all combinations of two (15 models), three (20 models), four (15 models) and five (six models) factors. Finally, we added all the factors

to fit the global model. For each model, the Akaike information criterion (AIC) value was calculated using correction for small samples sizes (AIC_c , Burnham & Anderson, 2002). The models were ranked according to their AIC_c and the best model has the smallest AIC_c value. Delta AIC_c (ΔAIC_c) was calculated to express the difference between each model and the best model. Akaike weights (w) were used to estimate the relative evidence for each model, and these can be interpreted as the probability that the model i is the best model for the observed data, given the candidate set of models. Since the global model for species richness indicated overdispersion ($c\text{-hat} = 1.93$), we used quasi-likelihood information criteria (QAIC_c) to identify appropriate statistical models for predicting the amphibian species richness. We tested the relationship between individual species and the habitat variables with binary logistic regression. The relationship between amphibian species richness, the number of species producing metamorphs and the habitat variables was tested with Poisson regression, using generalised linear models (GLM). All statistical procedures were implemented in R 2.10.1 (R Development Core Team, 2009).

Results

Wetland use by amphibians

Eight amphibian species were identified: *Triturus cristatus*, *Lissotriton vulgaris*, *Bombina variegata*, *Bufo bufo*, *Hyla arborea*, *Pelobates fuscus* (Laurentus, 1768), *Rana dalmatina* and *R. temporaria*. 'Ponds' and 'archaeological ditches' were generally less used by amphibians than 'drainage ditches' (Fig. 1). *Bombina variegata* used the 'pond' habitats more frequently than other amphibians, followed by *L. vulgaris*, *R. dalmatina* and *R. temporaria* (Fig. 1). *Triturus cristatus*, *B. bufo*, *H. arborea* and *P. fuscus* had the highest occupancy and reproductive success in 'drainage ditches' (Fig. 2). The cluster analysis grouped *H. arborea* and *P. fuscus* with *B. bufo* and *B. variegata* with *R. temporaria* and *R. dalmatina* with *L. vulgaris* according to their co-occurrence in the breeding habitats (Fig. 2).

We found a significant positive correlation between the number of aquatic habitats in a given year and the number of aquatic habitats colonised by adults for all species ($r > 0.89$, $P < 0.05$) except *H. arborea* and *P. fuscus* ($P > 0.05$). No relationship was found

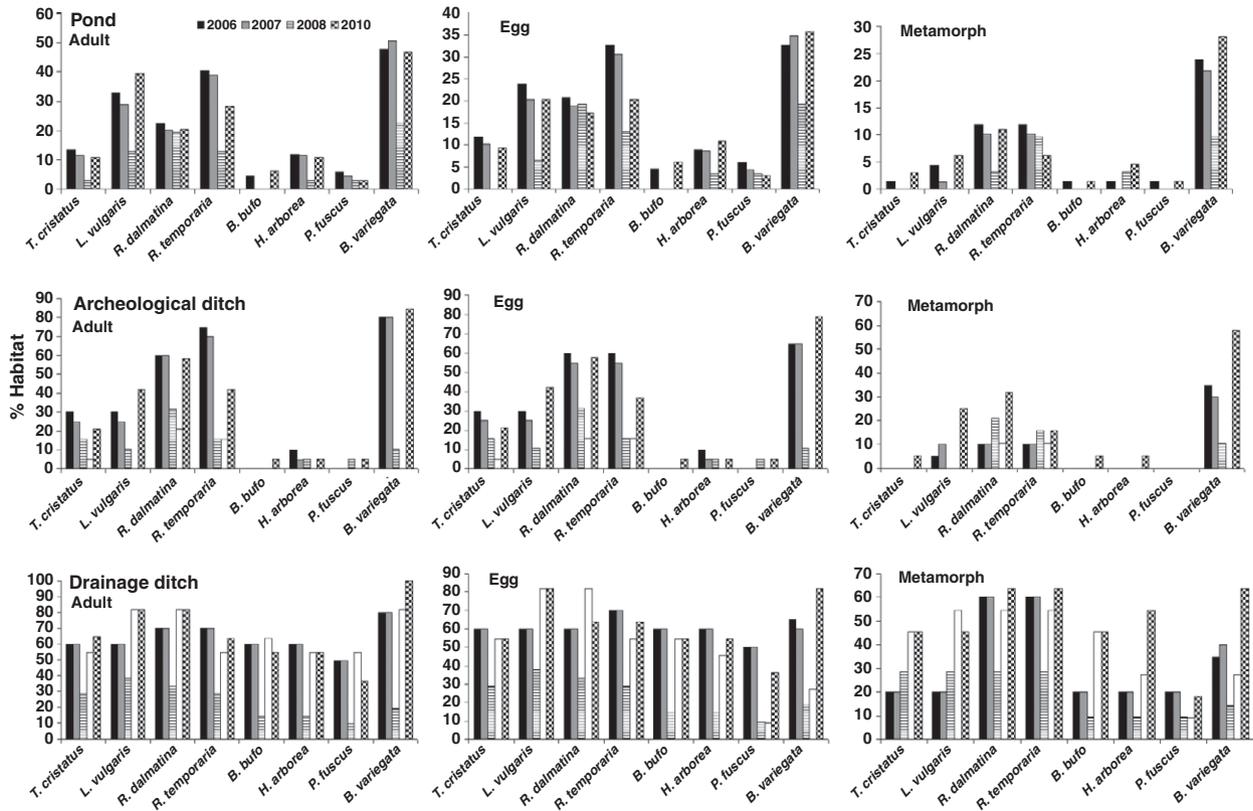


Fig. 1 Use of the three aquatic habitat types by amphibians in 2006–10. The year 2009 was not included because of the very low number of aquatic habitats (essentially only drainage ditches were filled).

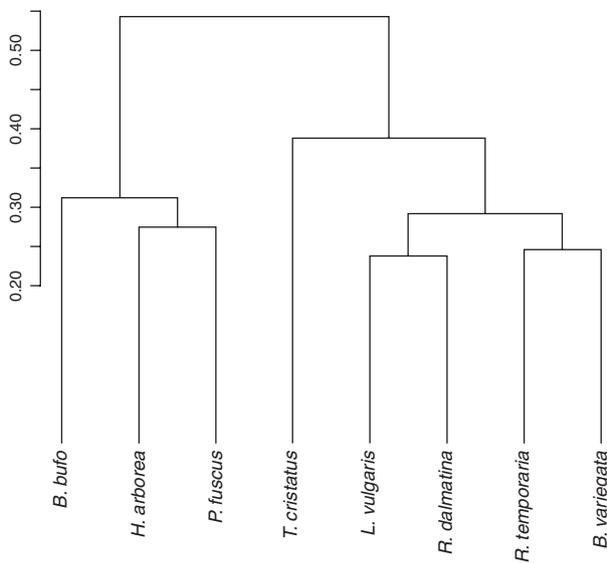


Fig. 2 Species co-occurrence in aquatic habitats based on cluster analysis.

between the movement distance of individual species and the number of habitats occupied by adults (Fig. 3).

The colonisation and extinction rates for aquatic habitats varied across species and time. For most species, extinction was higher than colonisation during 2007–09 (Table 2) and extinction was highest in 2008 and 2009. The number of aquatic habitats used by amphibians (except *B. bufo* and *P. fuscus*) doubled from 2009 to 2010 (Table 2). Except for *B. variegata*, no extinction events were recorded in 2009–10 (Table 2).

Modelling amphibian habitat use

The amphibian species richness varied significantly between the aquatic habitat types, from an average 4.75 (SD = 3.14) species in drainage ditches to 1.91 (1.85) in ‘archaeological ditches’ and 1.56 (2.03) in ponds. The number of species metamorphosing from the three aquatic habitat types followed the same pattern: 2.94 (3.07) in drainage ditches, 0.67 (1.25) in archeological ditches and 0.51 (1.20) in ponds.

The models best supported by the data included ‘year’ and ‘hydroperiod’ in each case (Table 3). The global model (containing all variables) was the best

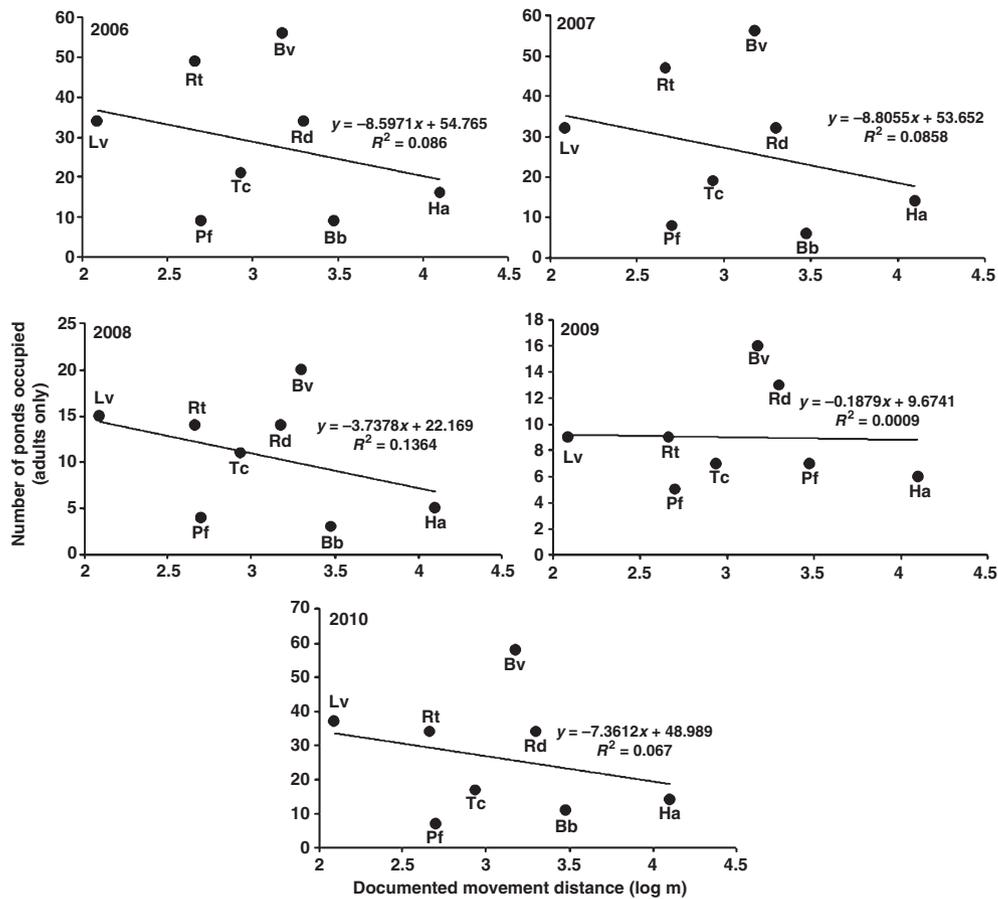


Fig. 3 The relationship between the movement distance (metres–log) and the number of aquatic habitats colonised by adults. Lv, *Lissotriton vulgaris*; Tc, *Triturus cristatus*; Rt, *Rana temporaria*; Rd, *Rana dalmatina*; Bv, *Bombina variegata*; Bb, *Bufo bufo*; Pf, *Pelobates fuscus*; Ha, *Hyla arborea*.

Table 2 Colonisation ('C') and extinction ('E') rates of species

	2006–07		2007–08		2008–09		2009–10		Overall		
	C	E	C	E	C	E	C	E	C	E	C–E
<i>Triturus cristatus</i>	0.09	0.23	0.16	0.53	0.00	0.28	1.71	0.00	0.49	0.26	0.23
<i>Lissotriton vulgaris</i>	0.02	0.14	0.18	0.50	0.06	0.20	3.22	0.00	0.87	0.21	0.66
<i>Rana dalmatina</i>	0.05	0.08	0.12	0.37	0.10	0.15	1.61	0.00	0.47	0.15	0.32
<i>Rana temporaria</i>	0.04	0.08	0.06	0.55	0.07	0.00	3.05	0.00	0.80	0.15	0.65
<i>Hyla arborea</i>	0.06	0.18	0.14	0.35	0.60	1.00	1.33	0.00	0.53	0.38	0.15
<i>Bombina variegata</i>	0.05	0.05	0.07	0.57	0.78	0.21	2.81	0.12	0.92	0.23	0.69
<i>Bufo bufo</i>	0.00	0.33	0.00	0.50	1.33	0.00	0.10	0.00	0.35	0.20	0.15
<i>Pelobates fuscus</i>	0.12	0.12	0.60	0.20	0.33	0.33	0.16	0.00	0.30	0.16	0.14

model for *T. cristatus*. For three species (*R. dalmatina*, *L. vulgaris* and *H. arborea*), the best model for the species richness and the number of species producing metamorphs included 'year', 'type' and 'hydroperiod'. For *R. temporaria* and *B. variegata*, the best model

included, in addition to 'year' and 'hydroperiod', also 'depth' and 'area'. The explained deviance of the best models ranged between 25.4 (*R. temporaria*) and 49.1 (number of species producing metamorphs), indicating a generally good predictive ability of the models.

Table 3 Model selection results. Models are ranked in a decreasing Akaike weight (w_i) order. For clarity, models with Akaike weight <0.05 are not shown. Statistics include the explained variance (D^2), the number of estimated parameters (K), the second-order Akaike information criterion corrected for small sample sizes (AIC_c), AIC difference (Δi) and Akaike weights (w_i)

Species	Model structure	D^2 (%)	K	AIC_c	Δi	w_i
<i>Bombina variegata</i>	Y + A + H + D	27.2	5	403	0.00	0.18
	Y + T + A + H	26.2	5	404	1.13	0.11
	Y + H	27.4	3	404	1.13	0.10
	Y + T + H	26.9	4	405	1.34	0.09
	Y + H + D	27.7	4	405	1.79	0.08
	Y + T + A + H + D	26.4	6	405	1.60	0.08
	Y + O + A + H	27.7	5	405	2.07	0.07
	Y + O + A + H + D	26.8	6	405	1.89	0.07
	Y + T + H + D	27.1	5	405	2.36	0.06
<i>Triturus cristatus</i>	Y + T + O + A + H + D	29.9	7	287	0.00	0.35
	Y + T + H + D	28.6	5	287	0.37	0.29
	Y + T + A + H + D	28.8	6	281	1.93	0.13
	Y + T + O + H	27.9	5	290	2.95	0.08
<i>Rana dalmatina</i>	Y + T + O + H	39.4	5	319	0.00	0.44
	Y + T + O + A + H	39.6	6	321	1.34	0.22
	Y + T + O + A + H + D	39.9	7	321	1.64	0.19
	Y + O + A + H + D	38.6	6	323	3.85	0.06
<i>Rana temporaria</i>	Y + O + A + H	25.4	5	402	0.00	0.50
	Y + O + A + H + D	25.5	6	404	1.77	0.21
	Y + T + O + A + H	25.8	6	404	2.33	0.16
	Y + T + O + A + H + D	25.9	7	406	3.99	0.07
<i>Lissotriton vulgaris</i>	Y + T + O + H	34.0	5	340	0.00	0.54
	Y + T + O + A + H	34.1	6	341	1.00	0.33
	Y + T + O + A + H + D	34.2	6	343	3.10	0.11
<i>Hyla arborea</i>	Y + T + O + H	36.8	5	220	0.00	0.50
	Y + T + O + A + H	36.9	6	222	1.90	0.19
	Y + T + O + A + H + D	37.0	7	224	3.47	0.09
	Y + T + O	34.8	4	225	4.44	0.05
	Y + T + O + D	35.3	5	225	4.66	0.05
Number of species producing metamorphs	Y + T + O + H	49.1	5	850	0.00	0.52
	Y + T + O + A + H	49.1	6	851	1.67	0.23
	Y + T + O + A + H + D	49.1	7	853	3.31	0.10
Species richness	Y + T + O + H	36.5	5	752	0.00	0.54
	Y + T + O + A + H	36.5	6	755	2.12	0.19
	Y + T + O + A + H + D	36.8	7	755	2.80	0.13
	Y + O + H	35.1	4	756	3.86	0.08

Y, year; T, pond type; P, predators; A, pond area; D, pond depth and H, hydroperiod.

The relationship between the habitat variables and amphibians (Table 4) showed that amphibians were always positively associated with the 'drainage ditch' character of the aquatic habitat, and in three cases (*B. variegata*, *R. dalmatina*, species richness), there was a negative relationship with the 'pond' character. There was no relationship with the 'area' of the aquatic habitat. Amphibians were positively related to 'depth', 'predator' and 'hydroperiod'. The 'year' effect was significant in two cases: *R. temporaria* (negative) and the number of species producing metamorphs (positive).

Discussion

In this study, we found that amphibians preferred waterbodies with longer hydroperiod for reproduction, these being represented in our study area by drainage ditches. The reproductive success of most of the species and the amphibian species richness was also higher in this aquatic habitat type. Of all the aquatic habitat types studied, drainage ditches had the longest hydroperiod every year. The hydroperiod of aquatic habitats may be a major constraint for amphibian occurrence and reproductive success

Table 4 The relationship between the amphibian species, species richness and the number of species producing metamorphs with the habitat variables and year

Habitat variables	<i>Triturus cristatus</i>	<i>Lissotriton vulgaris</i>	<i>Bombina variegata</i>	<i>Hyla arborea</i>	<i>Rana dalmatina</i>	<i>Rana temporaria</i>	Species richness	Number of species producing metamorphs
Type	Drainage ditch 1.91***	Drainage ditch 2.32***	Drainage ditch 0.80* Pond -0.50*	Drainage ditch 3.08***	Drainage ditch 1.21*** Pond -1.12***	Drainage ditch 0.69*	Drainage ditch 0.65*** Pond -0.20*	Drainage ditch 1.47***
Area	0.0007	-0.0001	-0.002	0.001	-0.0008	-0.003	-0.0002	-0.0004
Depth	0.05***	0.05***	0.04***	0.05***	0.05***	0.11***	0.02***	0.04***
Hydroperiod	0.11***	0.19***	0.19***	0.10***	0.19***	0.11***	0.05***	0.08***
Invertebrate predators	1.08***	1.22***	0.66***	1.15***	2.31***	1.03***	0.50***	0.84***
Year	-0.03	0.03	-0.006	-0.02	0.02	-0.19**	-0.01	0.14*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

(Semlitsch 2002; Hartel, Nemes & Mara, 2007) mainly through its effect on larval development and survival (Laurilä, 1998). We further found that those aquatic habitats with shorter hydroperiod (ponds and archaeological ditches) may also be attractive for amphibians in certain years (Fig. 1) although there was an overall negative association with the 'pond' character of the aquatic habitats and two species of amphibians and the species richness (Table 4). Species with longer larval periods (*T. cristatus*, *L. vulgaris*) and those preferring more permanent waterbodies for reproduction (the aforementioned newts plus *Bufo bufo*, *P. fuscus* and *H. arborea*) were more common in drainage ditches and had higher metamorphic success in these habitats. These species were also grouped by the cluster analysis (Fig. 2). Species with shorter larval period and phenotypic plasticity (*B. variegata*, *R. dalmatina*, *R. temporaria*) were more common and reproductively more successful in more ephemeral habitats than other species.

We found a significant positive correlation between the availability of the aquatic habitats (i.e. their yearly number) and the aquatic habitat use by adults, suggesting that amphibians are able to colonise newly available habitats. In contrast to the findings of Hecnar & M'Closkey (1997b), we found no relationship between the movement distance of amphibians and the number of aquatic habitats colonised. In fact we found slightly negative trends in every year (except 2009 when no trend was apparent), suggesting that species capable of longer movement distances occupy fewer ponds. Given that the terrestrial habitats do not limit dispersal and migration in our study area, it is possible that the quality of the aquatic habitats is an important limiting factor for their use by amphibians. Interpond movements are common in amphibian patchy populations (Sinsch, 1992; Petranka *et al.*, 2004; Hartel, 2008), and species able to move longer distances (possible also having larger home ranges) are more likely to be more selective regarding the pond quality at small spatial scale. This study shows that the hydroperiod of aquatic habitats is a good indicator of their quality for most amphibian species. In areas with high densities of aquatic habitats with variable hydroperiod, amphibians may opportunistically select breeding grounds by shifting their aquatic habitat use. This is realised by intense between-breeding pond movements and may result in increased reproductive success for some amphibian

species (Sinsch & Seidel, 1995; Petranka *et al.*, 2004; Hartel *et al.*, 2007; Hartel, 2008). Aquatic habitats can be located and qualitatively assessed using a number of cues (Miaud, 1990; Hopey & Petranka, 1994). A three-year recapture study conducted on *B. variegata* in a temporary pond system showed that the between-pond movement intensity and the movement distance varied yearly: in years with more precipitation, the individuals tend to move more frequently and cover larger distances (colonising ephemeral ponds as well), while in drier years, they tend to concentrate on more stable aquatic habitats and move less (Hartel, 2008).

The occurrence of several amphibians was positively related to the density of invertebrate aquatic predators (larvae of *Odonata* and *Coleoptera*). It is possible that adult amphibians and aquatic predators select breeding environments with similar features (e.g. more constant water bodies, see also Werner *et al.*, 2007a). Moreover, the temporary character of the aquatic habitats may keep predator density low (Wellborn *et al.*, 1996), and in such conditions, any negative effect of predators on amphibians may not be obvious. During our fieldwork, we often observed predation of amphibian larvae by aquatic coleopteran larvae (*Dytiscus* sp.), so the amphibian larval density may be sensitive to the density of insect predators. Amphibian larvae may show phenotypic and behavioural responses in the presence of predators (Teplitsky, Plénet & Joly, 2003) which can increase their survival when predators are present.

The aquatic habitat use was characterised by a high rate of turnover (i.e. gains and losses). The rate of pond population extinctions was higher than that of colonisations for most years, meaning the colonisation–extinction balance was mostly negative during the study period. However, the colonisation of new aquatic habitats at least doubled in 2010 relative to 2009 (Table 2) and the overall habitat occupancy in 2010 was much higher than those recorded in previous years. It is possible that this high colonisation rate and reproductive success in 2010 balanced the loss of the previous years. Climatic factors like precipitation may play an important role in determining population recovery in amphibians breeding in temporary ponds (Werner *et al.*, 2007b); for example, in 2010 (the year with the highest precipitation), the colonisation of new ponds and the reproductive success were higher

than in all previous years and also the reproductive success was the highest. Moreover, except for *B. variegata*, no local extinctions were observed in 2010. The local extinction of *B. variegata* in 2010 was much smaller than the colonisation (the gain-loss balance was positive) and may be caused by factors related to interspecific competition (Hartel, 2008). These results support previous studies and hypotheses (Pechmann *et al.*, 1991; Semlitsch *et al.*, 1996; Alford & Richards, 1999) that amphibian populations may be characterised by long periods of declines followed by sharp increases, in our case in habitat use and reproductive success.

In conclusion, the occupancy turnover of individual aquatic habitats was frequent in the studied amphibian populations inhabiting small temporary wetlands. Losses (extinctions) were more common than gains (colonisations). Climatic conditions such as precipitation were important determinants of turnover: a single year with abundant precipitation counterbalanced the losses registered in the previous years. Although hydroperiod was an important determinant of breeding habitat use for all the species studied, some species (e.g. *B. variegata*) performed better in aquatic habitats with short hydroperiod ('ponds') while others (e.g. *T. cristatus*) in aquatic habitats with longer hydroperiod ('drainage ditches'). Man-made temporary wetlands (drainage ditches) can represent important habitats for amphibians, and this needs to be considered in restoration activities; for example, filling in drainage ditches to stop water loss may harm amphibians because drainage ditches may contain the highest amphibian richness and the reproductive success of some species is highest in these wetlands. In these circumstances, creating dams along the drainage ditches and monitoring amphibian habitat use may be more efficient first interventions.

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