HERPETOLOGICAL JOURNAL, Vol. 11, pp. 41-51 (2001)

AMPHIBIAN BREEDING SITE CHARACTERISTICS IN THE WESTERN CARPATHIANS, POLAND

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The status of amphibian populations in the eastern part of the Western Carpathians, Poland, was investigated by assessing the number and ecological characteristics of breeding sites. Breeding populations of *Salamandra salamandra*, *Triturus cristatus*, *T. vulgaris*, *T. montandoni*, *T. vulgaris* x *T. montandoni* hybrids, *T. alpestris*, *Bombina variegata*, *Bufo bufo*, *Bufo viridis* and *Rana temporaria* were found. A total of 171 breeding sites together with their surrounding terrestrial habitats were examined for 11 environmental habitat parameters and data on presence/absence of other amphibians were recorded. A Canonical Correspondence Analysis (CCA) was performed to relate the species composition to the set of environmental variables. The first axis clearly differentiated *S. salamandra* from all other species, which were most clearly separated along the second axis. This second axis can be interpreted as a gradient of permanency and abundance of water vegetation. Generally, the CCA showed that environmental gradients were short, which reflects the limited range of habitats available for the amphibians in the area. *G*-tests revealed that two breeding assemblages could be distinguished. The first comprised newts of the genus *Triturus*, together with *B. variegata*; the second assemblage was composed of *Bufo bufo* and *R. temporaria*. The number of breeding species at a site was positively correlated with the surface area, "clay pit" habitat type and depth, but negatively with the "oxbow" and "stream" habitat types. Some 84% of all breeding sites were of human origin, the majority of them being small, transient water bodies such as wheel-ruts and roadside ditches. To keep the amphibian abundance in the study area at the present level, continuous human activity in creating and maintaining such suitable sites is necessary.

Key words: Amphibia, *Triturus montandoni*, breeding site, conservation, habitat choice, Western Carpathians

INTRODUCTION

Dramatic declines of populations of many amphibian species have been reported from all over the world (Wake, 1991; Blaustein, Wake & Sousa, 1994). The causes of these declines seem diverse and not fully understood. Changes in agricultural practices and road construction over the past 50 years have been major causes of loss of breeding sites in Western Europe (Beebee, 1996). Several formerly common and widely spread amphibian species are now considered rare, threatened or even endangered in Western Europe. In most cases the principal reason for these declines has been the loss of the breeding sites (Heusser, 1961; Prestt, Cooke & Corbett, 1974; Beebee, 1977; Oldham & Nicholson, 1986; Stumpel & Tester, 1992). The status of amphibian populations in Eastern Europe is not well known. Objective methods of measuring and monitoring amphibian populations have been applied only recently in some parts of Eastern Europe (Lars Briggs, pers. com.), but there are no published data which would enable comparisons with the data available for Western Europe. The general impression is that many habitats suitable for amphibians still exist in many parts of Eastern Europe due to the fact that environmental changes have been much less profound there than in Western Europe. On the other hand, much of Eastern Europe is now undergoing rapid development, with new patterns of land use being introduced, especially in agriculture. These may be expected to have a negative effect on amphibian populations.

The aim of our study was to assess the range of amphibian breeding site characteristics in an area which has preserved traditional forms of land use and which has a relatively rich amphibian fauna. Our study area was situated in the eastern part of the Western Carpathians (Magurski National Park, SE Poland; Fig. 1). Only traditional forms of agriculture have been practised here and since the end of World War II the area has been severely depopulated (Zajdel, 1997). Most of the land formerly used for agriculture and for human settlement has been undergoing the natural process of vegetational succession (Michalik & Michalik, 1997). We concentrated our survey on the quantitative description of breeding sites used by the local amphibians, and searched for associations between habitat characteristics and the presence of particular species. Number of breeding sites may be a better indicator of the present state and future prospects of amphibian populations than population size, which often shows large, natural fluctuations over the years (Pechmann *et al*., 1991; Green, 1997). Information on breeding site characteristics is important for conserva-

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tion purposes, as maintenance and creation of breeding sites have proven to be among the most effective ways of increasing the number and size of amphibian populations (Beebee, 1996).

Habitat selection by amphibian species has been studied extensively in Europe, but all these studies were restricted to the western part of the continent (e.g. Cooke & Frazer, 1976; Beebee, 1977, 1980, 1981, 1985; Fonseca & Jocque, 1982; Pavignano, Giacoma & Castellano, 1990; Denton, 1991; Ildos & Ancona, 1994; Marnell, 1998; Serra-Cobo, Lacroix & White, 1998). In regions which differ in geological and climatic conditions, these preferences may vary even within the same species. We follow previous studies in inferring a species' preferences by searching for associations between habitat characteristics and the presence of a species, even if the real preferences of the species depend on some unknown and/or unnoticed features of the environment.

One of the most common species in our study area is Montandon's newt (*Triturus montandoni*). This species has the most restricted distribution of all the European newt species (Arntzen & de Wijer, 1989), being confined to the Western and Eastern Carpathians as well as the easternmost part of the Sudeten Mountains. Local declines of this species have been reported (Kuzmin, 1994). The species is also considered as rare by several red-book lists (Baruš *et al*., 1988; Sytnik *et al*., 1988; Głowaciński, 1992) and it is included as a strictly protected species in Appendix II of the Bern Convention on the Conservation of European Wildlife and Natural Habitats. The distribution area of *T. montandoni* is limited to the territories of Romania, Ukraine, Slovakia, Poland and, marginally, the Czech Republic (Cogălniceanu, 1997). All these countries have been undergoing major political and economic changes, which are also likely to change the patterns of land use and agricultural practices. As the status of *T. montandoni* may be expected to suffer from these recent alterations, the need for description of its breeding habitats in an area where this species is still common is urgent.

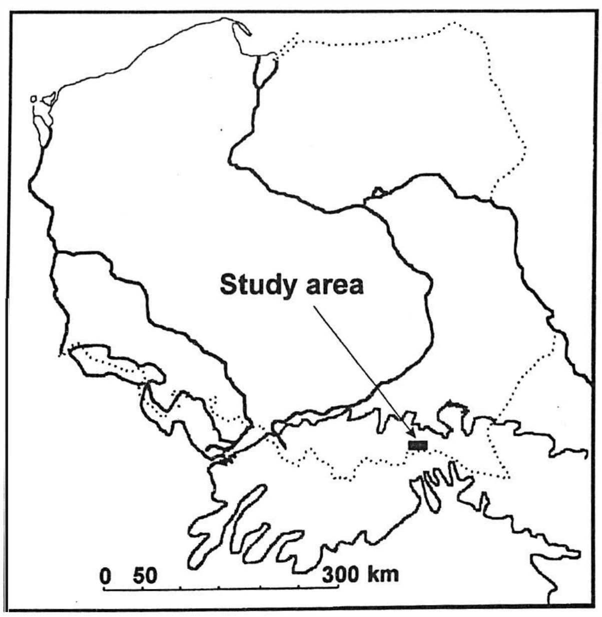

FIG. 1. Map of Poland with the study area indicated. A contour line at 300 m a.s.l. is shown.

Specifically, we wanted to answer the following questions: (1) Do the species distributed in our study area show associations with particular characteristics of the breeding sites described by the variables recorded? (2) Which of the measured variables can account best for observed amphibian breeding communities? (3) Do the amphibians present in the area form discernible breeding assemblages? (4) Is there any correlation between the features of the breeding site and the number of amphibian species at a site?

MATERIALS AND METHODS

DATA COLLECTION

The study area (Fig. 1) is situated in low-altitude mountains (maximum height 842 m a.s.l.). The growing season lasts 187 days/year on average. Mean (mean of daily means) temperature in July is 13.9°C; mean temperature in January is -7.7°C. Mean average rainfall ranges from 850 to 1000 mm, with 600-650 mm from April to September (unpublished recordings from a local meteorological station). Geologically, the area is homogeneous, and is situated on Flysch-type strata. The predominant soil type on mountain ridges and slopes is heavy clay (cambisoils), whereas alluvial deposits fill the river valleys (Skiba *et al*., 1999). The mountain ridges and slopes are almost entirely covered by mixed beech-fir forest; alluvial alder and willow woods are found along rivers and streams. Forests cover over 80% of the area (Michalik & Michalik, 1997). Arable land occupies only small areas in larger valleys. Traditional, non-intensive forms of agriculture predominate, especially pasture and hay-meadows (Dubiel, Gawroński & Stachurska, 1997).

The field work was conducted from April to July during three consecutive breeding seasons, in the years 1997-1999. Most of the identified breeding sites were visited during at least two breeding seasons. Our survey covered an area of about 450 square km. Valleys and ridges were much more extensively searched than wooded slopes, which were visited several times in different parts of the area. Such preliminary surveys showed that hardly any amphibian breeding sites were found on the wooded slopes, except for streams which were the breeding sites for *Salamandra salamandra*. Only the unsurfaced tracks on the slopes supported substantial numbers of amphibian breeding sites and for this reason they were searched intensively.

All the amphibian species recorded for this area lay their eggs in water and have aquatic larvae. A water body was recorded as a breeding site if either eggs or larvae were present, or – in the case of newts (genus *Triturus*) – if adults were present. Occurrence of adult

TABLE 1. Environmental variables recorded and the scoring system used.

Variable	Variable states
Altitude [m a.s.l.]	1, <400; 2, 400-499; 3, 500-599; 4, >600.
Breeding habitat	Wheel-rut, puddle or small pool, ditch, bomb hole, clay pit, fish pond, gravel pit, artificial basin, oxbow, stream.
Area [m²]	1, <1; 2, 1-2; 3, 2-10; 4, 10-100; 5, >100.
Depth [cm]	1, <10; 2, 10-20; 3, 21-50; 4, >50.
Bottom characteristics	Mineral, organic/mineral, organic
Substrate	Alluvial deposits, heavy clays (cambisoils) on Flysch-like sediments.
Aquatic vegetation	1, no vegetation; 2, along the edges only; 3, dispersed throughout the surface; 4, emergent and submerged vegetation over the whole area.
Turnover	Standing water, low turnover, high turnover
Permanence	1, ephemeral; 2, transient but not ephemeral; 3, permanent under normal climatic conditions; 4, permanent.
Surrounding terrestrial habitat	Mixed woodland; meadow/pasture, residual alluvial forest, village
Situation in relief	Valley, slope, ridge

newts in spring in a water body is strongly correlated with their reproduction there (pers. obs.). The presence of mature individuals, eggs and/or larvae was ascertained by visual inspection and/or dip-netting. Since both eggs and larvae of *T. montandoni* are indistinguishable from *T. vulgaris* under field conditions, the presence of either of these species was always verified by observation of mature newts. Presence of *T. cristatus* was established both by the examination of plants for the eggs, which could be identified as belonging to this species by their characteristic colour, size and shape, and by the presence of either larvae or mature individuals. For each anuran species a site was classified as a breeding site if eggs and/or tadpoles were found in it.

Very often in our study area amphibians used wheel-ruts as breeding sites. We therefore regarded sites that were more than 10 m apart as separate sites, as the chance of coalescence of such areas even after heavy rains was very small. For each breeding site the altitude a.s.l. was read from 1: 50 000 maps, and at the site we recorded the following characteristics: breeding habitat (i.e. the type of water body), area, depth, bottom characteristics, substrate, aquatic vegetation, turnover, permanence, surrounding terrestrial habitat and situation in relief (for details see Tables 1 and 2). The category "high turnover" was applied only to streams, "low turnover" designates such places as ditches, seepages and some oxbows. We classified the bottom characteristics in three categories: "mineral" – stones, gravel or clay; "organic" – bottom completely covered with decomposing plant material; "mineral/organic" – bottom partly covered by organic deposits. Breeding sites were situated on two types of substrate, either alluvial deposits (i.e. sand, gravel, stones) or heavy clays (cambisoils). We classified as "ephemeral" such places as very shallow puddles and flooded wheel-ruts formed after rain on unsurfaced tracks and without aquatic vegetation, which may, in the absence of rain, dry up very quickly (i.e. within a few weeks). Deeper wheel-ruts on roads and some ditches with aquatic vegetation situated in more damp surroundings – which indicated that they may last for a month or longer in the absence of precipitation – were classified as "transient". Stable water bodies which dried out in some years during the study were classified as "permanent under normal conditions". Under "surrounding terrestrial habitat", the terms "mixed woodland" or "residual alluvial forest" indicate that the water body was located no further than 100 m from the woodland. When no woodland was present at this distance, "meadow/pasture" or "village" was used. Water temperature, pH, conductivity and oxygen concentration were not measured because these parameters are highly dependent on inspection date, especially for small water bodies, which predominated in our study area. Additionally, we recorded whether each site was natural or of anthropogenic origin. We present these data in Table 2. In total, we sampled 171 breeding sites of amphibians (Table 2).

DATA ANALYSIS

Canonical Correspondence Analysis (CCA) was applied to investigate the relationship between amphibian breeding communities and the values of environmental variables (Ter Braak & Prentice, 1988). When the data collected include presence/absence of a species and environmental variables are coded in a nominal and/or ordinal scale, as was the case with our data, CCA is the most appropriate method for detecting relationships between species composition and environment (Ter Braak, 1986). The joint effect of the environmental variables on the species is represented in this method through a few ordination axes which can be considered as composite environmental gradients influencing species composition. CCA leads to an ordination diagram that simultaneously displays the approximate optima of the species in the low-dimensional (usually two-dimensional) environmental subspace, and environmental variables. Species optima are represented by points and direction and rate of change of variables by arrows on the diagram; nominal variables are represented by points. The ordination axes are weighted sums of the environmental variables. Altitude, aquatic vegetation, area, depth and permanence were coded as ordinal variables whereas all the others were nominal and were coded as dummy variables (Table 1). This resulted in a total of 30 variables included in the analysis. We performed forward stepwise analysis with CANOCO to establish which of the environmental variables were most important in shaping the composition of amphibian communities. The statistical significance was established by randomization tests with 999 permutations. Only variables with $P<0.05$ were included in the model and used for constructing the diagram (Table 3, Fig. 2). We also tested specific associations between some species or groups of species using 2 x 2 *G*-tests of independence (df = 1 in all cases).

To determine which environmental factors are useful in predicting the number of species reproducing at a given site, we performed forward stepwise multiple regression with the number of species recorded as a dependent variable and the variables listed in Table 1 as the independent ones (coded as for CCA). Computations were performed using STATISTICA (StatSoft, 1997) and CANOCO (Ter Braak & Šmilauer, 1998).

RESULTS

ENVIRONMENTAL ASSOCIATIONS

In the study area we found breeding sites of *Salamandra salamandra*, *Triturus cristatus*, *T. vulgaris*, *T. montandoni*, hybrids between the two latter species, *T. alpestris*, *Bombina variegata*, *Bufo bufo*, *Bufo viridis* and *Rana temporaria.* The most common species was *B. variegata* which occurred in 48.5% of the breeding sites. The second commonest species was *R. temporaria* (31.6%). The rarest species were *T. vulgaris* (3.5%), *T. cristatus* (2.9%) and *Bufo viridis* (1.8%) (Table 2). The widest range of breeding habitat types was used by *R. temporaria* and *B. variegata* (8 and 5 respectively). The narrowest range was found for *S. salamandra* and *Bufo viridis* (2 types for both) (Table 2).

The total range of amphibian breeding habitats in our study area is quite narrow, as can be seen from the CCA diagram (Fig. 2). As revealed by the randomization tests only 11 out of 30 environmental variables were significant in structuring the amphibian communities (Table 3, Fig. 2).

The first axis differentiated the breeding habitat of *S. salamandra* from all other species. This is hardly surprising, since all but one (93.3%) of its breeding sites were small mountain streams where no other amphibian species reproduced. Since other species were not separated along the first CCA axis it was not shown on the plot. The second axis showed the strongest correla-

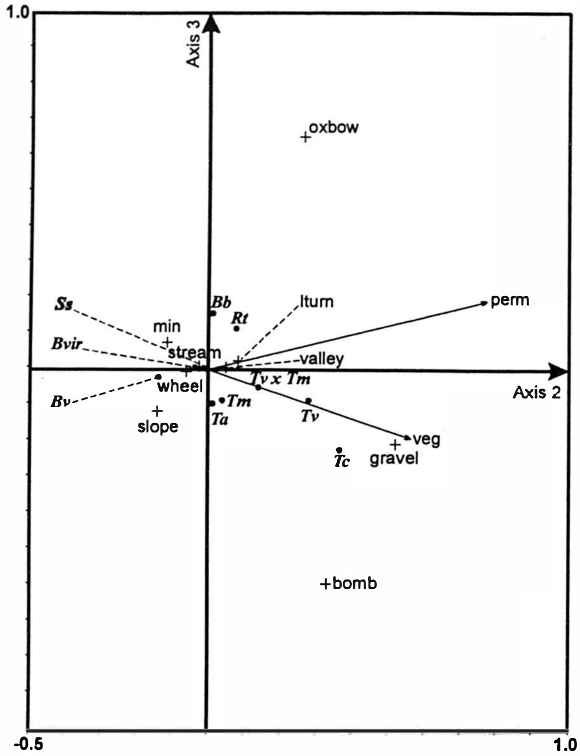

FIG. 2. Ordination diagram showing the positions of species (dots) and environmental variables in a plane of the second and third CCA axes. Nominal variables are shown as crosses, quantitative ones as arrows. Abbreviations: bomb, bomb hole; gravel, gravel pit, lturn, low water turnover; min, mineral bottom; perm, permanence; veg, aquatic vegetation, wheel, wheel-rut; *Ss*, *Salamandra salamandra*; *Tc*, *Triturus cristatus*; *Tv*, *T. vulgaris*; *Tm*, *T. montandoni*; *Tv x Tm*, hybrids between *T. vulgaris* and *T. montandoni*; *Bv*, *Bombina variegata*; *Bb*, *Bufo bufo*; *Bvir*, *Bufo viridis*; *Rt*, *Rana temporaria.*

tion with water habitat permanency and amount of water vegetation (Table 3) and contributed most to the species ordering (Fig. 2). The distribution range of species along the third CCA axis (explaining 11.3% of variance) is quite narrow. The most noticeable feature shown by this axis is that *Bufo bufo* and *R. temporaria* are grouped together, which is because these species were more often found in oxbows than the others (Fig. 2). The sum of the eigenvalues of the first four axes was 1.483 and accounted for 91.1 % of the total variance in the distribution of amphibian species at the sites studied with respect to the 11 significant variables (Table 3).

As can be seen from Fig. 2, more permanent and richly vegetated habitats were breeding places for *T. cristatus* and *T. vulgaris.* These two species were mainly found in larger and deeper water bodies like old gravel pits and bomb holes (*T. cristatus*). *T. vulgaris* was also found in richly vegetated wheel ruts and there was a clear geographic pattern in its distribution: this species occurred mainly in the northern part of the area adjacent to the lowlands and seems to have spread to the south along the Wisłoka river valley only (data not shown). In the case of *T. vulgaris* x *T. montandoni* hybrids, the main factor responsible for their occurrence was also the geographic location of the sites. Hybrids

TABLE 2. Characteristics of amphibian breeding sites in Magurski National Park. Abbreviations: *Ss*, *Salamandra salamandra*; *Tc*, *Triturus cristatus*; *Tv*, *T. vulgaris*; *Tm*, *T. montandoni*; *Tv x Tm*, hybrids between *T. vulgaris* and *T. montandoni; Bv*, *Bombina variegata*; *Bb*, *Bufo bufo*; *Bvir*, *Bufo viridis*; *Rt*, *Rana temporaria*. In the "Area" category NA is used for streams, for which the area could not be recorded.

	All sites		*Ss*	*Tc*	*Tv*	*Tm*	*TvxTm*	*Ta*	*Bv*	*Bb*	*Bvir*	*Rt*
	n	%	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*
% of all sites			8.8	2.9	3.5	26.9	4.7	26.3	48.5	21.6	1.8	31.6
n			15	5	6	46	8	45	83	37	3	54
Breeding habitat												
Wheel-rut	98	57.3	1	—	3	33	6	26	58	25	2	26
Puddle or small pool	10	5.8	—	1	—	2	—	3	6	1	—	5
Ditch	23	13.5	—	—	1	4	1	8	15	1	1	6
Bomb hole	3	1.8	—	1	—	3	—	3	—	—	—	—
Clay pit	3	1.8	—	1	—	1	—	3	3	1	—	2
Fish pond	2	1.2	—	—	—	—	—	1	—	2	—	2
Gravel pit	3	1.8	—	2	2	2	—	1	—	1	—	2
Artificial basin	2	1.2	—	—	—	1	—	—	1	—	—	1
Oxbow	13	7.6	—	—	—	—	1	—	—	6	—	10
Stream	14	8.2	14	—	—	—	—	—	—	—	—	—
All sites	171											
Altitude [m a.s.l.]												
<400	16	9.4	—	2	2	5	—	3	3	5	—	12
400-499	90	52.6	5	1	3	27	4	25	45	15	1	25
500-599	42	24.6	9	2	—	11	2	10	21	8	2	10
>600	23	13.5	1	—	1	3	2	7	14	9	—	7
All sites	171											
Area [m²]												
NA – coded as 0	14	8.2	14	—	—	—	—	—	—	—	—	—
<1	2	1.2	—	—	—	—	—	1	1	—	—	—
1-2	36	21.1	—	—	—	10	1	8	26	5	—	1
2-10	69	40.4	1	—	3	19	4	20	34	10	2	25
10-100	45	26.3	—	4	1	16	2	14	21	18	—	24
>100	5	2.9	—	1	2	1	1	2	1	4	1	4
All sites	171											
Depth [cm]												
> 10	6	3.5	2	—	—	2	—	1	2	—	—	1
10-20	125	73.1	12	1	2	32	3	26	68	21	1	32
21-50	30	17.5	1	1	2	6	5	12	13	11	2	15
>50	10	5.8	—	3	2	6	—	6	—	5	—	6
All sites	171											
Bottom characteristics												
Mineral	98	57.3	14	—	1	23	—	14	55	24	1	26
Organic/mineral	29	17.0	—	2	3	8	3	11	15	5	1	14
Organic	44	25.7	1	3	2	15	5	20	13	8	1	14
All sites	171											
Substrate												
Alluvial deposits	17	9.9	—	2	2	3	1	1	2	6	—	11
Heavy clays (cambisoils) on Flysch-like sediments	154	90.1	15	3	4	43	7	44	81	31	3	43
All sites	171											

TABLE 2. (continued...)

	All sites		*Ss*	*Tc*	*Tv*	*Tm*	*TvxTm*	*Ta*	*Bv*	*Bb*	*Bvir*	*Rt*
	n	%	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*
Aquatic vegetation												
No vegetation	19	11.1	14	—	—	1	—	1	3	—	1	1
Along the edges only	69	40.4	—	—	1	16	—	13	40	17	—	19
Dispersed on the surface	58	33.9	—	—	2	21	4	18	32	12	1	21
Emergent and submerged vegetation over the whole area	25	14.6	1	5	3	8	4	13	8	8	1	13
All sites	171											
Turnover												
Standing water	106	62.0	1	4	3	33	3	31	63	27	2	33
Low turnover	51	29.8	—	1	3	13	5	14	20	10	1	21
High turnover	14	8.2	14	—	—	—	—	—	—	—	—	—
All sites	171											
Permanence												
Ephemeral	14	8.2	—	—	—	2	—	2	11	2	—	—
Transient but not ephemeral	57	33.3	—	—	—	17	1	14	40	12	—	13
Permanent under normal climatic conditions	65	38.0	2	1	4	20	7	23	30	13	3	26
Permanent	35	20.5	13	4	2	7	—	6	2	10	—	15
All sites	171											
Presumed origin												
Natural	33	19.3	14	—	—	—	1	1	5	7	—	13
Man-made	138	80.7	1	5	6	46	7	44	78	30	3	41
All sites	171											
Surrounding terrestrial habitat												
Mixed woodland	84	49.1	15	—	1	20	4	24	37	15	2	17
Meadow/pasture	53	31.0	—	2	2	17	3	16	31	11	1	16
Residual alluvial forest	31	18.1	—	3	3	9	1	5	12	11	—	19
Village	3	1.8	—	—	—	—	—	—	3	—	—	2
All sites	171											
Situation in relief												
Valley	108	63.2	1	5	5	38	3	30	51	25	—	45
Slope	49	28.6	14	—	—	6	4	11	23	3	2	3
Ridge	14	8.2	—	—	1	2	1	4	9	9	1	6
All sites	171											

were found in the northern part of the area studied and in the Wisłoka river valley, where their parental species co-occur. In the ordination diagram sites populated by hybrids occupy an intermediate position along the second CCA axis between the two parental species.

In contrast to *T. cristatus* and *T. vulgaris*, the two remaining newt species (*T. alpestris* and *T. montandoni*) were more often found in less permanent sites with less abundant aquatic vegetation, as can be seen from the ordination diagram (Fig. 2) and Table 2. *T. montandoni* was a relatively common species in the study area, occupying 26.9% of all breeding sites. These were mainly water-filled wheel-ruts, with small surface area, with little or no turnover of water. This habitat type comprised 71.7% of breeding places for this species. Similar sites were occupied by *T. alpestris*; most often it was found breeding in water-filled wheel-ruts and roadside ditches (75.6% of all its breeding places) with no or little water turnover. Breeding sites of *T. alpestris* were found almost as often as those of *T. montandoni* (in 26.3% of recorded amphibian breeding places); in most cases these two newt species occurred syntopically.

B. variegata, the commonest species in the area (48.5% of all sites) occupies the opposite end of the environmental gradient represented by the second CCA

TABLE 3. Results of CCA. Significance of the individual variable contributions to the model (*P*), correlations of variables with CCA axes, and the variances explained by the axes.

Variable	*P*	Axis 1	Axis 2	Axis 3	Axis 4
		correlations of variables with axes			
Aquatic vegetation	0.043	-0.409	0.552	-0.186	0.171
Bomb hole	0.030	-0.035	0.230	-0.415	-0.182
Gravel pit	0.016	-0.048	0.501	-0.196	-0.343
Low water turnover	0.020	-0.150	0.243	0.073	0.367
Mineral bottom	0.002	0.190	-0.539	0.359	-0.374
Oxbow	0.001	-0.057	0.290	0.722	0.090
Permanence	0.001	0.320	0.766	0.192	-0.033
Slope	0.006	0.409	-0.343	-0.278	0.508
Stream	0.001	0.999	-0.023	0.009	-0.012
Valley	0.002	-0.304	0.322	0.032	-0.544
Wheel-rut	0.006	-0.256	-0.336	-0.032	0.181
Eigenvalue (λ)		0.932	0.226	0.183	0.142
Cumulative percentage of species-environment relation variance explained		57.3	71.1	82.4	91.1

axis; this signifies the least permanent and the least vegetated sites (Fig. 2). Table 2 also shows that *B. variegata* was found breeding most often in small, even ephemeral wheel-ruts and roadside ditches with standing water, mineral bottom and often very scarce aquatic vegetation or even none at all. Such habitats constituted 88% of breeding sites for this species.

R. temporaria was the second commonest species in the area (31.6% of all sites). It bred most often in wheel-ruts and roadside ditches (52.2% of its breeding sites), and also in oxbows (18.5%). *R. temporaria* quite often spawned in lentic water, 38.9% of all breeding sites had at least some water turnover; this can be seen also from the position of the species in Fig. 2. Generally in our study area *R. temporaria* only rarely reproduced in very shallow temporary pools.

Breeding habitats of *Bufo bufo* were similar to those of *R. temporaria.* It was the only other amphibian species, besides *R. temporaria*, found breeding regularly in oxbows (16.2 % of its breeding places, see also Fig. 2), although most often *Bufo bufo* spawned in larger wheel-ruts filled with water (67.6%) (Table 2).

TABLE 4. Species abundance at the breeding sites.

n of species	*n* of breeding sites	% of all breeding sites
1	90	52.6
2	50	29.2
3	20	11.7
4	6	3.5
5	3	1.8
6	1	0.6
7	1	0.6

Bufo viridis was found in three locations only, two were wheel-ruts and one was a ditch.

SPECIES ASSOCIATIONS AND ABUNDANCE

Associations between some amphibian species/ groups were tested using *G*-tests of independence. These tests revealed that *T. montandoni* often bred together with *T. alpestris* (G= 7.58, P<0.0001). All the newt species taken as a group were positively associated with *B. variegata* (G=10.86, P<0.0001), but no association was found between the newts and either *Bufo bufo* or *R. temporaria* (G=2.99, P=0.13). These two latter species often co-occured (G=3.08, P<0.0001). There was no significant association between the presence of *B. variegata* and other anuran species (G=1.48, P=0.22).

We also tested which environmental factors most significantly influenced the number of species breeding in a site. In more than a half of cases (52.6% of all the breeding sites) only one species was found (Table 4). The maximum number of seven species breeding in one locality was recorded at one site only. This breeding locality had some exceptional characteristics since it was formed by many closely-spaced wheel-ruts and pools which we treated as a single breeding site. Six species were found only at another breeding site, which was an old clay pit. Generally, as revealed by stepwise multiple regression, five environmental variables influenced the species abundance significantly. We found positive relationships between the number of species and area (b=0.346, P<0.005); "clay pit" habitat type (b=0.195, P<0.005) and depth (b=0.167, P<0.05). Negative relationships were found for the "stream" habitat type (b= –0.232, P<0.05) and "oxbow" habitat type (b=–0.192, P<0.05).

DISCUSSION

Out of 18 amphibian species found in southern Poland as a whole, in the area studied we recorded only nine. Our study area was outside the geographic and/or ecological range of such species as *Pelobates fuscus, Bombina bombina, Bufo calamita, Rana ridibunda, R. arvalis* and *R. dalmatina* (Juszczyk, 1987; Szymura & Rafiński, 1997; Hofman & Szymura, 1998). However, despite intensive search, we could not find such species as *Hyla arborea, R. lessonae* and *R. esculenta,* although the study area was located within the broad distributional limits of these species. We also failed to identify any environmental factor(s) which could explain their absence. It seems that *Bufo viridis*, which was recorded at only three sites, reaches its local distributional and/or ecological limits in the area.

The amphibians in the Magurski NP seem not to be as selective in breeding habitat choice as the same species studied in different areas of Europe (Pavignano *et al*., 1990; Ildos & Ancona, 1994; Serra-Cobo *et al*., 1998), though the methods of analysis used by the latter authors are not readily comparable to ours. One possible reason is that in our area only a narrow range of suitable habitats (breeding sites available) was present. On the other hand, we cannot reject the possibility that the relatively low selectiveness found in our study resulted from our arbitrary choice of environmental variables and the way we coded them. Narrow habitat range of amphibian breeding communities in the Magurski NP was revealed also by CCA analysis; both first and second axes were shorter than 1 SD.

The narrowest breeding niche was found for *S. salamandra,* which in the area studied bred almost exclusively in small mountain streams. But even for this species there are reports of it using seepages, roadside ditches, small puddles and wells as breeding places, especially in the more eastern part of the Carpathians (Świerad, 1988; personal observations).

The most successful species in the study area was *B. variegata*. It spawned even in very transient habitats like small pools, ditches and wheel-ruts which are the most common water bodies in the Magurski NP. Such small water bodies constituted 76.3% of all amphibian breeding sites there. The prolonged breeding season (April–August) and relatively rapid larval development period of *B. variegata* facilitates high reproductive success for this species even in transient pools (Rafińska, 1991). This species selects similar types of breeding habitats in other parts of its distribution (MacCallum *et al*., 1998).

More permanent roadside ditches and wheel-ruts left by heavy forestry vehicles were very often used as breeding sites by smaller species of newts: *T. vulgaris*, *T. montandoni* and *T. alpestris*. In such sites the newts often co-occurred with *B. variegata*, though the shallowest and the most temporary places used for breeding by *B. variegata* were typically avoided by the newts. The newts often occupied breeding sites where no other amphibian species was present (46% of all breeding sites for newts), but when another amphibian species was found at the same site it was usually *B. variegata* which co-occurred with newts in 33% of their localities. This resulted in a positive association between the presence of newts and *B. variegata.*

Generally, the four newt species reproduced in sites with at least some vegetation. Aquatic and at least partly submerged marginal vegetation provide the main substrates used for egg deposition by all newt species (Miaud, 1995). Both *T. cristatus* and *T. vulgaris* were rare species in our study area (found at five and six sites respectively), so we cannot generalize our findings with respect to environmental associations. Nevertheless, our data are in agreement with those reported by other authors (see below).

T. cristatus was found only in places with abundant submerged vegetation. However, this may be a secondary effect, because we found this species only in larger and more permanent waters which were usually rich in vegetation (the only habitat types we found this species in were gravel pits, a clay pit, a bomb hole and a large pool). Association with similar water bodies for *T. cristatus* was also reported from Western Europe (Beebee, 1975; Cooke & Frazer, 1976), but such a correlation was not found by Denton (1991). The specific requirements of *T. cristatus* may be the main cause of its being the rarest newt species in many areas of Europe and therefore the subject of serious conservation concern (Baille & Groombridge, 1996; Beebee, 1996). On the other hand, our own observations (unpublished) indicate that this species can show greater ecological plasticity in other parts of its distribution (the Polish Eastern Carpathians) as we have found it breeding there also in small water bodies such as roadside ditches and water-filled wheel-ruts.

T. vulgaris also bred in more vegetated places than the other two newt species (Table 2). Associations between aquatic vegetation and the presence of *T. vulgaris* were found by Fonseca & Jocque (1982), Ildos & Ancona (1994) and Marnell (1998). Although the association of *T. vulgaris* with abundant aquatic vegetation was clear, our observations should be treated with caution as this species was found at six sites only.

Our analysis demonstrated that *T. montandoni* and *T. alpestris* often occurred together, which may indicate that they share similar requirements. They seem not to depend so much on the presence of rich aquatic vegetation as *T. cristatus* and *T. vulgaris*. We did not find an obvious relationship between the presence of the woodland within 100 m of the breeding site and the presence of newts. In several studies a strong dependence by newts on the presence of forest or scrub habitat in the vicinity of the breeding site was found (Beebee, 1980, 1985; Pavignano, 1988). Lack of such an association in the present study may be explained by the general abundance of forest habitats in our study area.

Breeding sites of *T. montandoni* were found almost exactly as often as those of *T. alpestris*; nevertheless, the latter species was clearly not so abundant in Magurski NP as the former. We estimated the sizes of amphibian populations by dip-netting for some sites only but we do not report these here. The ratio of *T. montandoni* to *T. alpestris* was close to 2:1, as estimated from the data collected at 46 sites. This is most probably a geographical phenomenon, as in the Polish Carpathians the abundance of *T. alpestris* declines with the increase of *T. montandoni* towards the east (Szyndlar, 1980; Juszczyk, 1987; Świerad, 1988). The question of whether this is solely a result of the history of the postglacial colonization, or depends on some unknown environmental factor(s) along the west-east axis relevant to the requirements of these newts remains unanswered.

In our study area *Bufo bufo* and *R. temporaria* seem to have similar requirements and often spawned at the same sites. They usually used as breeding sites deeper wheel-ruts and roadside ditches, and seemed to avoid more shallow and transient water bodies. In our study area *R. temporaria* did not avoid sites with slowly running water (38.9 % of its breeding places).Together with *B. bufo,* they were the only amphibian species that often spawned in oxbows. This indicates that as early breeders, *R. temporaria* and *B. bufo* are perhaps more tolerant of relatively low temperatures during embryonic and larval development than other amphibian species occurring in Magurski NP. Although we have not collected any data on long term temperature fluctuations in the breeding places, oxbows – which are usually relatively deep and large water bodies – are generally cooler than small temporary pools.

The scarcity of larger water bodies is a salient feature of the area studied. Water bodies larger than 100 sq. m constituted only 2.9% of all breeding sites. Some of them may be of special importance for amphibian communities since they host large populations of several species. Being the most stable breeding habitats they probably serve as source populations for the whole metapopulation. For this reason such large multi-species breeding sites deserve special attention in the maintenance of amphibian populations. On the other hand, small water bodies – which in this area predominated – may give high reproductive success, especially in the years with high rainfall throughout the reproductive period. The impact of invertebrate predators can be significantly lower in smaller, more transient breeding sites, and it seems that at least some amphibian species actively choose smaller water bodies for breeding to avoid predation (MacCallum *et al*., 1998). Conservation measures for *Bufo calamita* in Britain showed that this species more successfully colonized smaller and shallower water bodies than larger ones, most probably because of lower predation pressure and weaker competition from other amphibian species (Beebee, 1996).

Many authors have reported the negative relationship between the presence of fish and that of amphibians (Beebee, 1977; Brönmark & Edenhamn, 1994; Ildos & Ancona, 1994; Aransson & Stenson, 1995), although a positive association was found for *B. bufo* by Beebee (1985). In our study area, still waters with fish were extremely rare (four oxbows and two fish ponds), so the impact of fish on amphibians could not be assessed.

Nearly all of the sites recorded in the study area were of human origin (84.2%). Natural sites were confined to streams – which were only used for breeding by *S. salamandra* – and the oxbows, where the only species reproducing were *R. temporaria* and *B. bufo*. To prevent the reduction of amphibian population size, and to maintain the whole biodiversity of this and similar areas, the active protection of man-made habitats is very important. The commonest types of amphibian breeding habitat in the Magurski National Park were water-filled wheel-ruts and roadside ditches found along tracks and minor roads. Any modernization of roads used for local traffic, especially in woods, will cause a dramatic decline of the number and size of amphibian populations. For example, the existence of *T. montandoni* in Magurski NP is almost entirely dependent on the presence of roadside ditches and wheel-ruts. Similar environmental conditions seem to predominate in many of the mountainous regions of Eastern Europe. In order to preserve the present status of amphibian populations there, active maintenance of existing – and creation of new – breeding sites is needed. Such conservation practices have proved to be very successful for the preservation of amphibian breeding populations in Western Europe (Laan & Verboom, 1990; Arntzen & Teunis, 1993; Fog & Briggs, 1997; Beebee, 1996).

ACKNOWLEDGEMENTS

We would like to thank Dr Jacek M. Szymura for helpful suggestions on the manuscript. The paper benefited from comments made by the editor and two reviewers. Dr Z. Dzwonko introduced us to CCA analysis. A. Bieniek, J. Dziadosz, W. Kilarski, M. Krawczyk, K. Rogowski, K. Sarnecka and A. Szydło helped with data collection in the field. The work was in part financed by grant PD 9017 from the Magurski National Park.

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Accepted: 8.11.00