BREEDING PHENOLOGY AND SPATIO-TEMPORAL DYNAMICS OF POND USE BY THE YELLOW-BELLIED TOAD (*BOMBINA VARIEGATA*) POPULATION: THE IMPORTANCE OF POND AVAILABILITY AND DURATION

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Abstract. We analysed the spatial and temporal variation of breeding habitat availability and use by a yellow-bellied toad population in a mixed deciduous forest between 2003–2005. During this period, the number of temporary ponds was highly variable. Toads tended to exploit newly created breeding habitats or those of which hydroperiod increased due to precipitation. Ponds with intermediate and long duration were preferred for reproduction. We found no evidence of predator avoidance behaviour (aquatic invertebrates and newts) or reproductive failure in ponds containing aquatic predators. Ponds located in sunny patches of the forest were preferred for reproduction. We suggest that ponds that act as sinks in years with low precipitation could contribute to the demography of toad populations in rainy years, when their hydroperiod increases.

Key words: spawning period, yellow-bellied toad, habitat availability

INTRODUCTION

Temporary ponds represent a rich environment for aquatic organisms inhabiting them (Williams 1987) and significantly contribute to the increase of biodiversity both at the local and regional level (Semlitsch 2000). Amphibians represent ideal organisms to study adaptations to temporary ponds due to their frequent occurrence in these water bodies.

Pond-breeding amphibians have aquatic (eggs and larvae) and terrestrial (metamorphs and adults) life stages. It is known that the quality of the larval environment (pond quality) has important effects on the fitness of terrestrial adults (Scott 1990, 1994). Moreover, the aquatic stages of pond-breeding amphibians have the highest mortality rates in comparison with other stages (reviewed by Hartel 2005). Therefore, it is not surprising why strategies should be directed towards increasing the survival probability of larvae until metamorphosis. The reproductive success of temporary pond breeders largely depends on both pond availability and different strategies used to maximize breeding efficiency in temporary ponds. The response of amphibian larvae to a decrease in habitat quality is through accelerating the developmental rate (phenotypic plasticity) (Newman 1992). The larval growth and development rate and, therefore, the adaptive plastic response of amphibian larvae to environmental conditions are influenced by biotic factors such as food availability (Newman 1994), predation (Skelly & Werner 1990; Kruuk & Gilchrist 1997; Petranka *et al*. 1998) and larval density (Scott 1990, 1994; Semlitsch & Caldwell 1982). According to the model of Wilbur and Collins (1973), there is a threshold larval body size/developmental stage that must be attained by larvae to be capable of initiating and completing metamorphosis in response to environmental deterioration (Morey & Reznick 2000). Moreover, it was shown that the growth of amphibians at the larval stage has a significant influence on their size and age during metamorphosis that in turn affects adult body size and fecundity (Wilbur & Collins 1973; Semlitsch *et al*. 1988; Semlitsch 1987; Scott 1990, 1994). Large, rapidly growing larvae that metamorphose at a larger size become larger metamorphs and finally larger adults than small, slow-growing larvae (Semlitsch 1987).

By exploiting newly created aquatic habitats that act as sinks (Pulliam 1988) during dry years, the larval crowding could be avoided and the rate of larval growth and development could be increased. This could contribute to the demography of the population by increasing the fitness of adults and natality at the population level. Adult amphibians may also use strategies to increase

the probability of larval survival. Species, such as yellow-bellied toad (*Bombina variegata*), that prefer temporary ponds for reproduction reproduce repeatedly during the season, in synchronization with rainfalls when ponds are filled (Barandun 1992; Barandun & Reyer 1997a, b), and have a short larval period. This way, reproductive success can be maximized in temporary ponds. The main objective of this paper was to present the breeding phenology and spatio-temporal dynamics of habitat use by a *Bombina variegata* population in a deciduous forest habitat during the period 2003–2005. Specifically, we formulated the following hypotheses: (i) toads frequently prefer transient ponds to those of ephemeral or permanent character, (ii) to maximize reproductive success, breeding adult toads tend to occupy newly created temporary ponds, (iii) ponds located in sunny patches of the forest are preferred to shaded ponds.

Using allelomorphological features as the coloration of the belly (the so-called spot score developed by Szymura & Barton 1991), the studied population was categorised as a *Bombina variegata*-like hybrid population (Mara & Hartel, unpubl.). For the lack of genetic data (molecular markers were developed by Nürnberger *et al*. 2003), the studied population was considered as belonging to the species *Bombina variegata*.

MATERIAL AND METHODS

Study area and data collection

The study area is situated in a mixed deciduous forest in the middle of the Târnava Mare Valley, central part of Romania (Fig. 1), and has an area of approximately 1.5 km² (N46.2298, E24.7946 are the coordinates of the largest pond situated in the central-eastern part of the area). The *B. variegata* population reproduces in a temporary pond network formed by a number of 75 ponds (Fig. 1) with a high variety of hydroperiods ranging from four days to two years (Hartel & Nemes 2006). The average pond area is 22 m² (range: 1–250 m², SD = 44), and the depth averages 23 cm (range 3–100 cm, SD = 21) (Hartel & Nemes 2006). Temporary ponds are situated at about 500 m above sea level.

Data collection was started in 2003, beginning with pond formation after snow and ice melting (first part of February). In 2003, we spent 21 days, and in 2004, 24 days in the field. Every day all ponds in each field were carefully searched for adult toads, larvae and eggs. Moreover, the presence of aquatic vegetation, vertebrate (*Triturus cristatus*, *Triturus vulgaris* and *Natrix natrix*) and invertebrate predators (Odonata and Dytiscus) was also noted (see below).

We used a number of habitat variables to describe temporary ponds and their surroundings. The abiotic variables used were: pond area (m²), maximum depth (cm), the state of a temporary pond in a light patch. The latter was scored as '1' or '0' for sunny or shaded ponds, respectively. Also, the ponds were included in one of the following three categories considering their hydroperiod: ephemeral (usually dries up within two weeks after filling (scored as 1), transient (usually dries up one or two times per season (May – early September)) (2) and permanent (regularly holds water throughout the toad activity season) (3) (Hartel *et al*. 2005). The biotic variables considered were: aquatic vegetation (present-absent (scored as '1' for presence and '0' for absence)), invertebrate predator larvae (see above) (1–0) and newts (see above, scored as predator larvae). Ponds were grouped into the following categories: ponds never used by toads (scored as 0), ponds with adult toads present (1) and ponds used for reproduction (2). Further, we grouped ponds considering the intensity of reproduction during the three year period: ponds that were used for reproduction for only year (scored as 1), two years (2) and three years (3). The temporary ponds system is used for reproduction by five other amphibian species: *Triturus cristatus*, *T. vulgaris*, *Rana dalmatina*, *R. temporaria* and *Hyla arborea*.

Data analysis

We compared average ponds recorded by the nonparametric Kruskal-Wallis test, followed by the multiple comparison Z-test. The ratio of ponds used for repro-
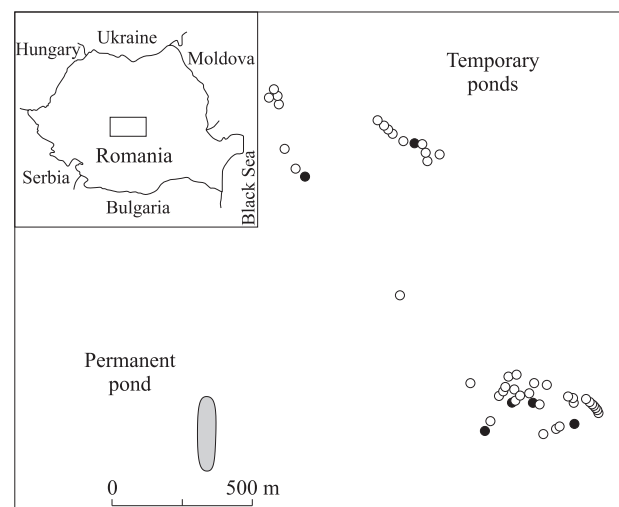

Figure 1. Map of the study area with a permanent pond and the temporary pond system. Black dots represent those ponds from which metamorphosis occurred in three consecutive years (Hartel & Nemes 2006).

duction was compared by the normal approximation of the binomial distribution computing the Z-score and the associated *p*-value.

The presence of toads was recorded as a Bernoulli distributed variable, 0 when absent and 1 when present. The sample size was restricted to a relatively small number of ponds, thus a logistic regression approach frequently used in similar cases was not suitable in this case. A total of eight predictor variables were considered: two continuous (area and depth) and six binary (the presence of: invertebrate predators, newts, light patch; the nature of a pond: ephemeral, transient and permanent). To reduce the high dimensionality of the data matrix, we performed a Principal Component Analysis (PCA) based on nonlinear iterative partial least squares. The number of components extracted was determined using eigenvalues (greater than 1) and the predicted variation. How well the PCA model repre-

sented a variable was measured by the modelling power that ran from zero (irrelevant) to one (relevant). The existence of outliers that might pull the model toward themselves was checked by Hotelling's T² and the square of the prediction error (Q_i). The component scores were used as input for one-way ANOVA. As light is particularly important, light conditions were compared by estimating a 95% confidence interval (CI) for differences between the ratio of lighted ponds of the second pond category. If zero falls within the confidence interval we can conclude that the data is consistent with the null-hypothesis of no differences.

RESULTS

The course of breeding

In 2003, there were two clearly distinguishable spawning periods, both covering 16 days. The first spawning period was from 25 April to 10 May and the second from 25 July to 7 August. During both periods, the increase in precipitation was the main cue triggering spawning (Fig. 2).

In 2004, there were three loosely distinguishable spawning periods, all covering 42 days: the first lasted between 18 April and 6 May, the second between 20 June and 6 July, and the third from 21 to 8 July. The amount of precipitation seemed to have played a role in triggering the spawning seasons in 2004 (Fig. 2). We were not able to estimate the start and length of the spawning season in 2005. The percentage of ponds in which successful metamorphosis occurred increased by 40%, 65% and 90% in each of the three years, respectively. In 2003, metamorphosis was restricted to the most durable ponds.
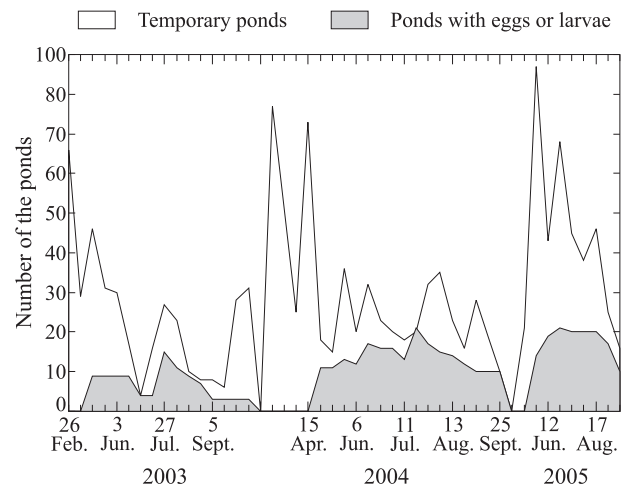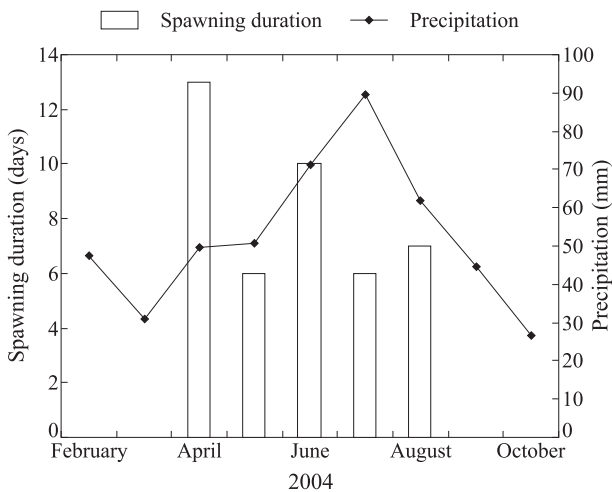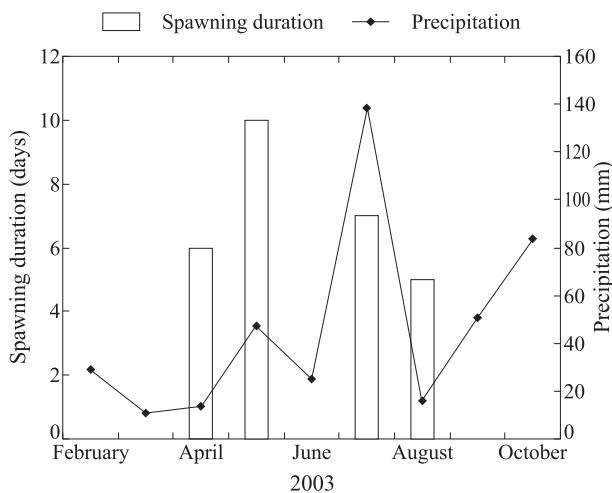

Figure 2. Breeding periods and their duration; precipitation in 2003 and 2004.

Figure 3. Fluctuations in the number of ponds within and between the seasons during the three years of study.

Dynamics of pond number and pond use

The average amount of precipitation in toads' active period (April–August) was larger in 2004 and showed a smaller variation (52.17 mm/m² SD = 16.6) than in 2003 (48.02 mm/m², SD = 52.17). A total number of ponds and the number of ponds used for breeding showed large within-season and between-year fluctuations (Fig. 3). Significant differences were found between the three years regarding the average number of ponds available (H = 9.4, df = 2, p = 0.009). Multiple comparisons showed significant differences between the years 2003–2005 (Z = 2.98, p = 0.008) and 2004–2005 (Z = 2.48, p = 0.03), whereas no significant differences were recorded between 2003–2004 (Z = 0.68, p = 0.71). Thus, the average number of ponds was largest in 2005. The average number of ponds used for breeding differed between the years (H = 23.79, df = 2, p < 0.0001), although multiple comparisons revealed a different pattern. The average number of ponds used for breeding did not differ between the years 2004–2005 (Z = 1.77, p = 0.22). The average number of ponds was significantly higher in 2004 than in 2003 (Z = 3.45, p = 0.001) and in 2005 than in 2003 (Z = 4.59, p < 0.0001).

A larger percentage of ponds was used for reproduction in 2004 (57%, 95% CI: 52–62) than in 2003 (34%, 95% CI: 28–40) and 2005 (38%, 95% CI: 33–43). The difference was significant both between 2003–2004 (Z = -5.84; p < 0.0001) and 2004–2005 (Z = -5.08; p < 0.0001). No significant differences (Z = -1.03, p = 0.3) were obtained between 2003–2005.

Factors affecting breeding habitat use

All variables exhibited a significant effect on the presence and reproduction of toads in the ponds. PCA analysis resulted in four new variables that together explained 91% of initial variation (Table 1). Although the last two components individually explained less than 10% of variation, they offered no inference about the ecological factors affecting pond use by toads. All initial variables were well represented. There were both positive and negative loadings on both principal components. The first axis offered inferences about all variables except the transient nature of some ponds, the transient character being represented jointly with light conditions by the second axis (Table 2). The frequency of pond use was well delimitated on the first axis. Ponds that were used for three consecutive years had the highest absolute score value, the lowest being recorded at ponds inhabited for two years. These two had negative scores, while ponds where no toads were found and those inhabited for one year had positive scores. The first component showed significant differences between the four pond types regarding their intensity of use by *Bombina*: ponds not used at all, ponds where *Bombina* was present for one year, two years and three consecutive years ($F_{[3, 47]}$ = 36.09; p < 0.0001). A pairwise comparison showed that ponds used by *Bombina* for three years were significantly different from those that were used for only one or two years, and those not used at all. The difference between ponds used for three years and those used for one year was close to significant (p = 0.09) (Table 3).

Table 1. Characteristics of the principal components on the six measured variables (R²X – variance explained, Q² – predictive variance).

Component	R²X	R²X (Cumul.)	Eigenvalues	Q²	Q² (Cumul.)
1	0.573	0.573	6.30	0.538	0.538
2	0.178	0.751	1.96	0.722	0.871
3	0.098	0.849	1.07	0.835	0.978
4	0.064	0.914	0.71	0.906	0.998

Table 2. Factor loadings for the first two principal components on the six variables and the modelling power of PCA analysis.

	PC1	PC2	Power
Pond area (m²)	-0.626	-0.455	0.740
Pond depth (cm)	-0.859	-0.019	0.743
Permanent	-0.811	-0.206	0.920
Transient	0.805	-0.407	0.920
Ephemeral	-0.157	0.719	0.982
Light patch present	-0.622	0.634	0.992
Newts present	-0.842	-0.309	0.946
Invertebrate predators present	-0.907	-0.133	0.937

Table 3. Descriptive statistics for the first two principal components grouped by the pond colonization factor and the results of post-hoc Scheffé F-test. 0 = toads absent, 1 = adults present for one year, 2 = adults present for two years, 3 = adults present for three years.

		PC1					PC2		
Pond use	Mean	SE	L95% CI	U95% CI	Pond use	Mean	SE	L95% CI	U95% CI
0	1.87	0.36	1.13	2.61	0	-0.78	0.32	-1.43	-0.12
1	1.46	0.41	0.64	2.29	1	-0.16	0.36	-0.89	0.56
2	-0.13	0.45	-1.03	0.77	2	1.18	0.39	0.37	1.98
3	-3.17	0.38	-3.93	-2.40	3	0.13	0.33	-0.54	0.81
	0	1	2	3		0	1	2	3
0		0.910	0.013	<0.001	1		0.66	0.005	0.29
1			0.090	<0.001	2			0.116	0.94
2				<0.001	3				0.27

The scores of the second axis differed significantly only between ponds used for two years and those where no toads were found (Table 3).

Significant differences were observed in the characteristics of ponds used for reproduction and those containing adults, but not used for reproduction, as well as those not inhabited by toads (Table 4). Significant differences were detected on both axes (PC1: $F_{[2, 48]} = 17.3$; $p < 0.0001$; PC2: $F_{[2, 48]} = 3.87$; $p = 0.027$). On the first axis, differences were significant between ponds used for reproduction and those containing adult toads, but not used for reproduction (PC1: $F_{[2, 48]} = 17.3$; $p < 0.0001$). The second axis showed significant differences only between ponds used for reproduction and those not used at all (PC2: $F_{[2, 48]} = 3.87$; $p = 0.027$). On the first axis, ponds used for three years had positive scores, the other two categories negative; the second axis was negative for ponds not used and positive for ponds used for two years and those used for only one year, neither of them differs significantly from zero (Table 4). Ponds not used by toads for reproduction were shallow ephemeral and shaded. In contrast, ponds used for reproduction had significantly better light conditions than ponds where only adult toads were present ($p_{diff} = 0.48$ [CI: 0.21–0.74]). Ponds used for spawning contained invertebrate predators and newts. Ponds with toads absent and those used for one-year reproduction had a small area and were shallow, mostly ephemeral and shaded. Ponds used for two-year reproduction were larger and deeper and were situated in sunny patches compared with ponds that contained no toads ($p_{diff} = 0.7$ [CI: 0.46–0.93]) and those used for one-year reproduction ($p_{diff} = 0.45$ [CI: 0.13–0.76]). Ponds where toads reproduced for three consecutive years were large and deep, with a long hydroperiod (of a transient and permanent character) and the frequent presence of newts and invertebrate predators. Their light conditions were considerably better than those of ponds with no toads present ($Pr_{Diff} = 0.78$ [CI: 0.58–0.97]) or used for one-year reproduction ($p_{diff} = 0.53$ [CI: 0.25–0.80]). However, light conditions did not differ significantly between ponds used for two- and three-year reproduction ($p_{diff} = 0.08$ [CI: 0.00–0.38]).

Table 4. Descriptive statistics for the first two principal components grouped by the reproduction factor and the results of post-hoc Scheffé F-test. 0 = no toads present, 1 = adults present, but no breeding occurred, 2 = breeding occurred.

		PC1					PC2		
Pond use	Mean	SE	L95% CI	U95% CI	Pond use	Mean	SE	L95% CI	U95% CI
0	1.87	0.51	0.85	2.89	0	-0.78	0.34	-1.47	-0.09
1	1.38	0.65	0.06	2.69	1	0.09	0.44	-0.79	0.98
2	-1.50	0.376	-2.26	-0.74	2	0.40	0.25	-0.11	0.91
	0	1	2			0	1	2
0		-	0.838	<0.001	1		-	0.303	0.0281
1				0.001	2				0.832

DISCUSSION

Pond availability and breeding: strategies to maximize efficiency?

There was a considerable variation in the number of ponds available for reproduction both within the seasons and throughout the years. Whereas the overall number of available ponds did not differ in 2003 and 2004, the average number of ponds was larger in 2005 than in the previous years. A more constant distribution of precipitation could maintain some temporary ponds for a longer period of time than a large amount of precipitation followed by a longer period of drought. This happened in 2004. In 2005, the average overall number of ponds was larger than in the previous years due to the large amount of precipitation throughout the year.

As expected, toads used a flexible breeding strategy to exploit efficiently breeding ponds. The number of breeding periods was not fixed: there were two breeding periods in 2003 and three in 2004. The partition of the breeding season in several cohorts triggered by rainfall is considered an adaptive reproductive strategy in *Bombina variegata* (Barandun 1992; Barandun & Reyer 1997a, b, 1998; Gollmann *et al*. 1998): the reproductive success (i.e. the survival of larvae until metamorphosis) could be increased if reproduction starts immediately after the beginning of pond filling. This is natural, because *B. variegata* females show continuous egg development (Böll 2002). Observations from 2004 (this study, Fig. 2) and 2006 (T. Hartel, pers. observ.) suggest that egg deposition periods are not always preceded by an increase in the amount of rainfall; moreover, an increase in precipitation does not always initiate egg deposition. This suggests that egg deposition could be under endocrine control. High ecological plasticity regarding feeding strategies in *Bombina variegata*-like hybrids was found by Sas *et al*. (2005). It was experimentally shown that early and synchronized reproduction (i.e. after pond formation or filling) can be more advantageous for larval growth and development than late breeding, because of competition and predation pressure from the larvae of early breeders (Morin *et al*. 1990; Lawler & Morin 1993; Petranka & Thomas 1995). Toads tend to exploit newly formed breeding habitats or those that have became useful for reproduction due to the increased hydroperiod. An overall increase in the percentage of ponds with successful metamorphosis (from 40% to 90% in 2003 and 2005, respectively) shows that toads efficiently exploit breeding habitat resources in order to maximize their breeding success. The use of newly formed, no more than one year old reproductive sites by *Bombina variegata*

was observed in Germany and France (Wagner 1996; Möller 1996; Jahn *et al*. 1996). The tendency to use more ponds for reproduction shows the evidence that toads assess the quality of ponds and as soon as it increases ponds are used for reproduction.

Factors affecting pond use by toads

Our results show that ponds that are most frequently used for reproduction and where metamorphosis is successful have a transient and permanent character. Pond desiccation frequently causes catastrophic mortality of tadpoles, which affects the spatio-temporal dynamics of populations (Pechmann *et al*. 1991; Semlitsch *et al*. 1996). In a long-term study, Petranka *et al*. (2004) found that an adequate density of ponds may result in the opportunistic selection and shifting of breeding grounds depending on their disturbance history. Areas with high variability of ponds in terms of their hydroperiod and adequate density may occur only rarely in a region. Thus, amphibians often have no possibility to choose optimal ponds. The toads in this study area are in a similar situation.

Ponds preferred by toads for reproduction also contain predator newts (*Triturus vulgaris* and *T. cristatus*) and insects (Odonata, Dytiscidae). The presence of newts was restricted only to permanent and transient ponds. Moreover, reproductive failure due to predation was never observed in the studied ponds (neither in toads, nor in newts). These results are in agreement with the findings of Barandun and Reyer (1997b): larval survival is higher in ponds containing predators. Amphibians display predator-induced morphological (i.e. deeper tail muscles) and behavioural (i.e. increased refuge use and low activity) changes in the presence of predators (Teplitsky *et al*. 2003, see Kruuk & Gilchrist 1997; Vorndran *et al*. 2002 for *Bombina* sp.). These changes could increase the survival probability of larvae under a high risk of predation.

As expected, ponds situated in sunny patches of the forest were preferred more often by toads for reproduction. Environmental temperature is positively correlated with the rate of growth and metamorphosis (Newman 1994; Denver 1997). Shallow, warm and productive ponds allow a faster larval development and quick attainment of the developmental threshold (Wilbur & Collins 1973; Morey & Reznick 2000).

In conclusion, our results show that yellow-bellied toads in the study area prefer sunny, intermediate and long-duration ponds for reproduction. These ponds contain both invertebrate and vertebrate predators (newts). In years with low precipitation, breeding is restricted to the most durable ponds. When new ponds become available for reproduction, toads tend to use

them. The percentage of ponds with successful meta-morphosis increase in years with a larger amount of precipitation. Temporary ponds that act as sinks during dry, unfavourable years provide good breeding habitats during rainy years. Thus, the source-sink character of breeding habitats of *B. variegata* is dependent on precipitation. The aspects of the described breeding ecology of this population show similarities with other *B. variegata* populations found in western Europe.

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Geltonpilvių kumučių (*Bombina variegata*) dauginimosi fenologija ir vandens telkinių panaudojimo veisimuisi erdvinė bei laikinė dinamika: balų gausos ir egzistavimo trukmės svarba

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Santrauka

Geltonpilvės kūmutės populiacijos veisimosi ypatumai, susję su erdviniais ir laikiniais jos vandens buveinių pokyčiais buvo tirti mišriame lapuočių miške 2003–2005 metais. Tuo laikotarpiu išdžiūstančių mažų vandens telkinukų skaičius buvo labai nepastovus. Tarp geltonpilvių kūmučių pastebėta tendencija daugintis naujai susiformavusiuose vandens telkinukuose arba tuose, kurie neišdžiūvo ilgesnį laiką dėl gausesnio kritulių kiekio. Dažniausiai reprodukcijai buvo pasirenkamos ilgai neišdžiūstančios arba vidutinio vandeningumo balos ar kūdros. Buveinėse, kuriose buvo aptikti vandens plėšrūnai, apsaugančio nuo plėšrūnų elgesio ar nesėkmingos reprodukcijos atvejų nebuvo pastebėta. Dauginimuisi dažniausiai buvo pasirenkami telkinukai, esantys saulėtuose miško plotuose. Manoma, kad vandens telkiniai, kurie neišdžiūsta ištisus metus net esant sausringiems orams, skatina rupūžių populiacijos augimą ir lietingais metais, kai vandens telkinukai neišdžiūsta ilgiau.