North-Western Journal of Zoology Vol. 4, No. 1, 2008, pp.79-90
[Online: Vol.4, 2008: 13]

# Movement activity in a *Bombina variegata* population from a deciduous forested landscape

Tibor HARTEL

Mihai Eminescu Trust, Str. Cojocarilor 10, 545400 Sighisoara, Romania,
E-mail address: asobeka@yahoo.com

**Abstract.** *Bombina variegata* is a temporary pond breeder, strictly protected under the Habitat Directive (Annex II). The persistence of its populations highly depends on the ability of individuals to locate and efficiently use for reproduction the various temporary ponds. This can be realized with permanent movements through the landscape. In this study I explore the effect of precipitation on the movements of *B. variegata* in three years (2003-2005), based on mark-recapture of individuals. The average between-pond distances covered by toads for the whole study period was 161 m whereas that of females was 172. Movements were recorded between 66 ponds out of up to 75 existing in the area. The yearly average movement distance by females showed a clear increase with the amount of precipitation in the active season, from an average of 93 m (SD = 88.94) in 2003 to 251.35 m (SD = 164.07) in 2005. The recaptures were the most frequent from ponds being at approximately 200 m from each other. The exchange of individuals significantly decreased with the increasing distance between the ponds. There was a positive relationship the SVL females and the distance from the pond to which they moved. The maintenance of an adequate density of ponds may decrease the isolation by distance between the aquatic habitats and may facilitate the toad`s movements through the landscape.

**Key-words**: *Bombina variegata*, movement distance, precipitation

## Introduction

The study of the animal movement activity (migration and dispersal) is currently an important research objective at both theoretical (i.e. Diffendorfer 1998, Adler & Nuernberger 1994) and real population level (i.e. Nuernberger 1996, see the review of Bowler & Benton 2005) including amphibians (Semlitsch 2008). These movements have multiple reasons such as competition, predation, aggression, disease, avoidance of inbreeding, and the spatial and temporal variation of the habitat quality (see for example Hansson 1991, Diffendorfer 1998, McCarthy 1999, Matthysen 2005, Gros et al. 2006). Although spatial movements may be risky and often may end with death if the individual doesn`t reach a proper habitat in time, it may be still better to assume this risk than to stay in the local population where the low quality of environment decreases the fitness, reproductive success and/or increase the probability of loss (Roff 1975, Diffendorfer 1998). The dispersal, if it is caused by local increased density (i.e. Matthysen 2005), will increase the importance of large populations in the metapopulation dynamics (Hansson 1991).

The distribution of organisms with complex life cycles such as pond-breeding amphibians (Wilbur 1980) is frequently constrained by the quality and distribution of the breeding habitats. This is because the environmental conditions, especially hydroperiod and predation, strongly influence the egg and larval survival (Wellborn et al. 1996). It was shown that amphibian larvae are able to accelerate their growth and development (phenotypic plasticity) to increase the probability of survival (i.e. metamorphosis) when the aquatic conditions become harsh (Wilbur & Collins 1973, Newman 1992). Another key of survival in such cases is the ability of adults to locate and permanently evaluate the quality of the breeding habitats. A poor ability to select high quality breeding habitats will result in increased reproductive failure if these habitats are „diluted" between low quality habitats, the organisms being also more sensitive to habitat loss (Pulliam & Danielson 1991). Many amphibian species are adapted to efficiently explore for reproduction, aquatic habitats of which quality is often unpredictably changing in time. Amphibians are able to locate the old and new breeding habitats (Joly & Miaud 1993; Dall`Antonia & Sinsch 2001; reviewed by Sinsch 1991) and evidences suggest that they may be able to assess their quality (Hopey & Petranka 1994, Petranka & Hayes, 1998, but see Laurila & Aho, 1997). Due to their permeable skin that requires certain climatic/microclimatic conditions for its function (Feder & Burggreen, 1992), the success of these movements are highly dependent on the environmental conditions especially those linked to the microclimate.

The Yellow Belied Toad (*Bombina variegata*) is a good candidate for studies of movement activity because: (i) It is adapted to breed in temporary ponds, habitats with highly varying hydroperiod (Barandun 1992, Barandun & Reyer 1997a, b, Barandun & Reyer 1998, Hartel et al. 2007a). Because of the temporary character of the breeding ponds, the reproductive success depends on intensive movements and knowledge of the breeding area. (ii) It reproduces more times during the active season, often synchronized with rainfall that fills the ponds (Hartel et al. 2007a), (iii) The Yellow Bellied Toad is in decline in various parts of Europe, and is listed on the Annex II of the Habitat Directive (92/43/EEC). This species is common in the Târnava Mare basin (Hartel et al. 2006) and its breeding habitats are under threat due to drainage activities (Hartel et al. 2007b). Therefore, studies are needed in order to better understand the spatial habitat use of this species and to predict how this protected species will be affected by the reduction of the density of temporary ponds and their hydroperiod.

The aim of this paper is to present:

(i) The intensity of between-pond movements of the individuals, based on individual and pond-specific marking and recapture.

(ii) To explore the relationship between the movement activity and the weather conditions in males and females.

(iii) To explore the relationship between the movement distance and body size of toads.

**Materials and methods**

The studied area has about 3 km² and is situated on a forested (mixed deciduous) plateau in the middle section of the Târnava Mare basin, Romania (N46.2298, E24.7946, altitude above sea level around 500 m) (Fig.1). This study site was described in detail in Hartel et al. (2006, 2007a). The *B. variegata* population reproduces in a temporary pond network consisting from up to 75 ponds (Fig.1) with a high variety of hydroperiod ranging from four days to more than two years. The average pond area is 22 m² (SD = 44), and the depth averages 23 cm (range 3 - 100 cm, SD = 21) (Hartel & Nemes 2006). This group of temporary ponds is situated on an area of approximately 1.5 km². Every pond was located with a handheld GPS (4-9 m accuracy). The distances between the ponds that were close to each other (i.e. within 25 m) were estimated also visually besides GPS.

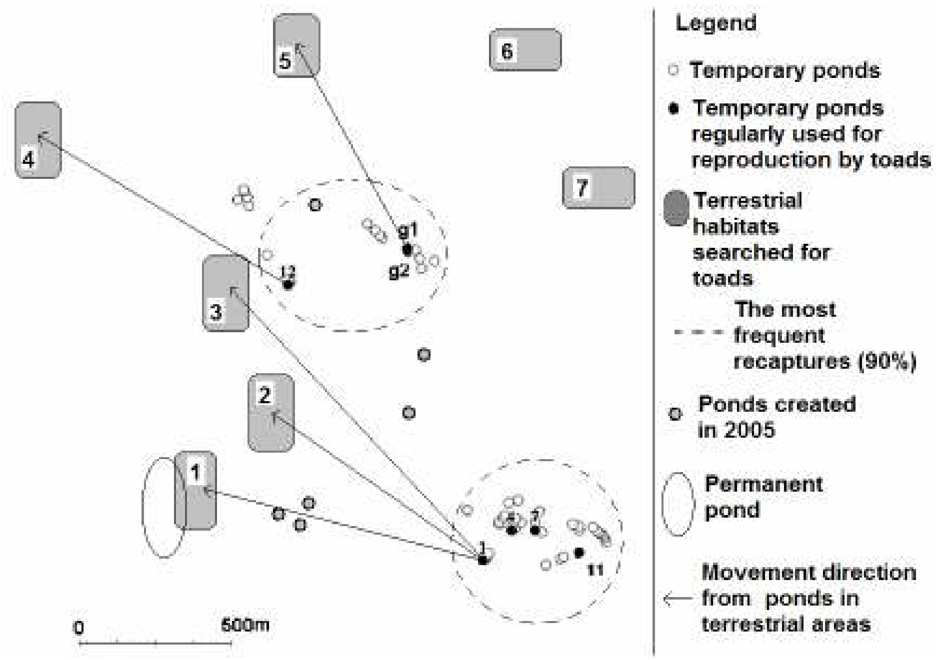


**Figure 1**. The map of the study area. The temporary pond cluster is delimited as being the breeding area of toads. The terrestrial areas searched for roaming – dispersing individuals and those sites where recaptured toads were found are also showed. The numbers within the symbols representing the terrestrial habitats, explained in the Methods section. The black points represent those ponds that were used for reproduction in all years.

Data collection regarding the temporal fluctuation of the ponds and searches for toads (capture-recapture [Hartel & Nemes, 2006]) and eggs and larvae [Hartel et al. 2007a]) was started in 2003. In 2003, we spent 21 days in the field; in 2004, 24 days whereas in 2005 we spent 8 days with monitoring habitats and searching for marked toads from previous years (Hartel & Nemes 2006).

In 2004 and 2005, careful searches were conducted in seven terrestrial sites (situated at up to 500 m distance) from the breeding area (Fig.1). As amphibians prefer humid patches as terrestrial habitats (humidity being a vital necessity for the normal physiological function of their skin [Feder & Burggreen, 1992]) the searches in the terrestrial sites were conducted in these habitats. Temporary ponds with reproductive activity were never recorded in these sites. Three of these sites were ruderal areas (sites 1, 4, 7 in the Fig.1) situated along or near dirt roads and agricultural lands. One habitat (site 5) was situated in and open patch in the forest, two sites (sites 2 and 3) were situated at the forest edge, along a temporary spring, that originates from the forest (I assumed that these springs are used by toads for dispersal) and one site (site 6) was forested. The observations of the toads in these sites were made in afternoon hours by search in undercovers (in the forested areas) or open areas. These searches were most intense after rains because the toads were more active. The newly created temporary ponds inside or outside the breeding area (six ponds in 2005) were also regularly searched for toads (Fig.1).

A total of 395 toads were individually marked in 2003, following the method described by Hero (1989). In 2004, 413 toads were marked using pond specific marks (i.e. by clipping one toe of each toad) (Hartel & Nemes, 2006). The breeding behaviour was not affected by the toe removal, and no signs of infection were found after the toe clipping (Hartel & Nemes 2006). This suggests that the toads were not affected in short term by this marking technique. The body condition of the toads was also not affected by the toe clipping (Hartel & Nemes 2006). Six ponds, with the longest hydroperiod, were used for reproduction every year (2003-2005) (black circles in the Fig.1).

The snout vent length (SVL) (0.1 mm precision) was measured in 27 recaptured toads from this population in the second part of July-first part of August, 2005 (Hartel & Nemes 2006).

I considered that movements between ponds occurred when an individual captured and marked in one pond was recaptured on a different pond. In this case the approximate distance between the ponds (in meters) was measured and used to estimate the movement distance. The analysis of between pond movement distances was made in two steps. First, I compared the overall median movement distances between the ponds for the males and females separately. For this analysis I pooled together the between pond migration distance data gathered from the three years of study and used Mann-Whitney U test for comparison. The grouping variables were the „males" and „females" and the dependent variables were the movement distance data (in meters). Second, I tested if there were significant differences in the median values of the between pond movement distances in the males and females in the three years separately. Kruskall-Wallis ANOVA was used for this purpose. In this analysis, the individual movement distances recorded for males and females in a particular year were used as dependent variables. The grouping variable in this analysis was the variable „year" (i.e. 2003, 2004 and 2005). The relationships between the SVL of the individuals and the movement distance was tested with the linear regression for 27 recaptured individuals measured in 2005.

The precipitation data were gathered from the hydrological station from Albeşti, from around 5 km distance from the studied population.

**Results**

The average amount of precipitation in the toads active season increased through the years. Thus, the year 2003 was the driest (48 l/m$^2$), the precipitation amount slightly increased in 2004 (67 l/m$^2$) whereas the year 2005 was the most rainy (128 l/m$^2$). The number of toads marked and recaptured for 2003 and 2004 is shown in Table 1. The great majority of the marked individuals were recaptured only once during this period, and five individuals were captured more than once. No subadults marked in 2003 were recaptured in 2004 or 2005, and no subadults marked in 2004 were recaptured in 2005.

The proportion of resident males (i.e. those recaptured in the same ponds as where they were marked) was: 31% (= 9 individuals out of the 29 recaptured) in 2003, 52% (i.e. 11 out of 21 recaptured) in 2004 and 33% (i.e. 6 individuals) in 2005 (Tab.1). In the females 42% were resident in 2003, 27% in 2004 and 29% in 2005 respectively (Table 1). In the case of subadults, 50% were resident in 2003 and 47% were resident in 2004.

The median between-pond distance moved by male toads for the overall study period was 122 m and the average was 161 m (SD = 162.13) (Min-Max = 6-562 m). In the case of females the median of the movement distance was also 122 m whereas the average was 172 m (SD = 127.56) (6-600 m). The differences between the movement distances were not significant ($Z$ = -1.58, $P$ = 0.11).

Movements were recorded between 66 ponds out of up to 75 existing in the area. The descriptive statistics of the yearly between-pond movement distances of males and females are presented in Table 2. The differences between the median movement distances were not significant in the case of males (Kruskal – Wallis test, $H$ = 5.07, $P$ = 0.07) and were significant in the case of females ($H$ = 9.06, $P$ = 0.01).

**Table 1.** The yearly recaptures of the Yellow Bellied Toads in the studied population.

| | Recaptures: total (migrating) | |
|---|---|---|
| **Year (individuals marked)** | 2003 | 2004 |
| 2003 (Total marked: 395) | 68 | - |
| Male (180) | 29 (20) | - |
| Female (154) | 19 (8) | - |
| Subadult (61) | 20 (6) | - |
| 2004 (Total marked: 413) | 62 | 60 |
| Male (170) | 22 (23) | 21 (10) |
| Female (188) | 40 (25) | 26 (19) |
| Subadult (55) | 0 | 13 (5) |
| 2005 (No marking) | 13 | 29 |
| Male | 1 (0) | 17 (12) |
| Female | 12 (6) | 12 (11) |
| Subadult | 0 | 0 |

The toads moved mostly within the two groups of ponds, the recaptures being the most frequent from ponds at approximately 200 m from each other (Fig.1 & 2). Both the number of interactions (in terms of recapture events) (Spearman $r$ = -0.81, $P$ = 0.04, n = 6 distance categories) and the number of ponds where recaptures were found (Spearman $r$ = -0.88, $P$ =

0.01, n = 6) strongly decreased as the distance between the ponds increased (Fig.2). Recaptures of six toads (two males and four females) were made in terrestrial habitats (Fig.1) at distances up to 1300 m from the ponds where they were marked (Fig.1).

The relationship between the SVL of the males and the migration distance was not significant in the case of males (linear regression, $R^2$ = 0.0004, $F_{[1, 8]}$ = 0.003, $P$ = 0.95). In the females, the relationship was positive and highly significant, the SVL accounting for 40% of the variation in female movement distance ($R^2$ = 0.40, $F_{[1, 15]}$ = 10.01, $P$ = 0.006).

**Table 2.** The descriptive statistics of the between pond movement distances of the male and female toads in the three years of study.

| | Between pond movement distances (m) | | | | |
|---|---|---|---|---|---|
| | Mean | Median | Min | Max | SD |
| Males | | | | | |
| 2003 | 123 | 67 | 10 | 562 | 164.16 |
| 2004 | 181 | 165 | 10 | 562 | 150.37 |
| 2005 | 166 | 69 | 6 | 562 | 191.61 |
| Females | | | | | |
| 2003 | 93 | 71 | 20 | 260 | 88.94 |
| 2004 | 155 | 122 | 6 | 537 | 102.39 |
| 2005 | 251 | 220 | 50 | 600 | 164.07 |

## Discussions

In this study, it was possible to assess the movement activity of the Yellow Bellied Toads in changing climatic conditions. The low rate of recapture was already discussed and compared with other studies that were based on toe clipping (Hartel & Nemes 2006). The most plausible reason is that the toads were roaming in the terrestrial habitats (as found by another population studied by Barandun & Reyer 1998) and their recapture was not possible in these conditions. The lack of juvenile recaptures in the years following their marking can be explained by (i) High subadult dispersal (emigration) from this population. Gollmann & Gollmann (2000) found that Yellow Bellied Toads may disperse at considerable distances in the first 2-3 years of their postmetamorphic life. They suggest that the benefits of the early dispersal may be the gaining knowledge about the landscape and the distribution of the resources in it. The fact that 5 adults were recaptured in the years 2006 and 2007 (Hartel *personal observations*) that were marked as juveniles in 2003-2004 suggest that the juveniles may stay longer periods of time in terrestrial habitats within or outside the breeding area (making impossible to locate them with the methods used in this study) and some of them may return for reproduction as adults. Thus, the assumption of Gollmann & Gollmann (2000, 2005) seems to be valid at least for some individuals from this population. (ii) The subadult mortality also may be a cause of low recapture. I exclude the possibility of toad mortality due to the marking methodology (Hartel & Nemes 2006). The design of this research makes difficult to assess the relative importance of these two factors on the recapture of the juveniles. The juvenile stage is considered to be the main dispersal stage in many pond breeding amphibians (i.e. Gill 1978) including European temporary pond breeders such is *Bufo calamita* (Sinsch 1992) and *B. variegata* (Beshkov & Jameson 1980, Gollmann & Gollmann 2000, 2005).

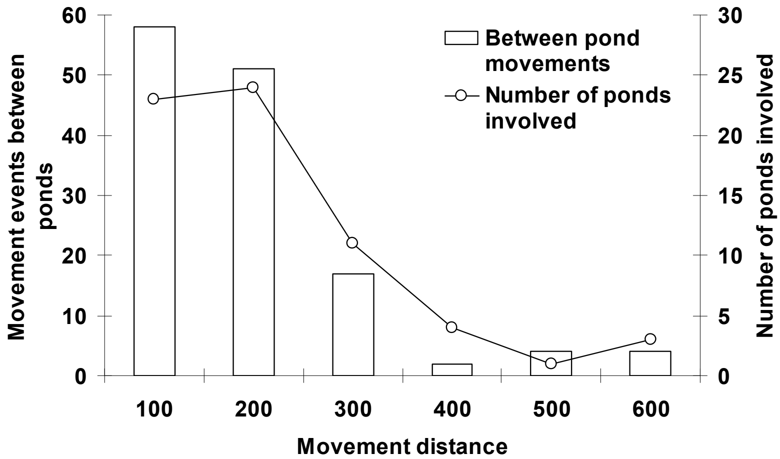


**Figure 2.** The number of movement events between pond, and the number of ponds from which recaptures were made at different between pond distance categories (m).

The results regarding the between pond migration distances of toads are close to those found by other studies on this species. For example Gollmann & Gollmann (2000) and Gollmann et al. (2000) reported a mean 190 m for males (maximum 980) and 150 m for females (maximum 600 m) in a mixed forest scattered with open grassland habitats in Austria. Beshkov & Jameson (1980) recorded smaller migration distances along a stream from the Balkan Mountains (Bulgaria): 64 m for males and 20 m for females. Barandun & Reyer (1998) recorded maximum between pond distances of 240 m in a habitat consisting mainly of open area in Switzerland. All the above mentioned studies, including this one, may seriously underestimate the long distance movements outside of the breeding area in this species due to the research design used. In this study, the frequency of movements between ponds significantly decreases with the increasing distance between the ponds, most of the between pond movements being recorded at ponds being within 200 m distance from each other. The great majority of the ponds were visited by toads (66 from the maximum 75 recorded in that period), but only a small number of them was used for reproduction (maximum 21 in 2004 [Hartel et al. 2007a]). Hartel et al. (2007a) found that some ponds that are not suitable for reproduction in dryer years (i.e. 2003) may assure suitable habitats for reproduction in rainy years when their hydroperiod is longer (2005). Moreover, the newly created suitable ponds (by heavy machineries [Fig.1] or long rainy periods) were quickly colonized and used for reproduction (Hartel et al. 2007a). The small temporary wetlands not suitable for reproduction may act as stepping stones for toads if they are maintained at adequate densities (Semlitsch & Bodie 1998).

The recaptures from the terrestrial areas at high distances, suggest that toads may move outside the breeding area (temporary pond cluster) probably in search for new breeding habitats. Marchand (1993) observed short distance movements in *B. variegata*, of around 20-30 m among summer habitats in Wesertal, Germany. Longer migrations of up to 650 m were observed during the fall migration on the way to the wintering habitats. The results of this study, in line with that suggested previously by Marsh & Trenham (2001) suggest that the movement distance by toads may be underestimated if only the between pond movements are considered. The fact that the recaptures in terrestrial habitats were made on the western part of the breeding area (Fig.1) suggest that the air humidity (the wind blows from the western part, from the direction of the Târnava Mare river and a permanent pond) and / or the humid patches (Hazzell 2003, Hartel et al. 2008) may influence the movement (dispersal) direction in this toad. It was showed that amphibians use the humidity gradients for orientation, including location of breeding ponds (Joly & Miaud 1993, Dall`Antonia & Sinsch 2001). The maximum movement distance of this toad may be seriously underestimated because I have searched only the terrestrial habitats up to 500 m from the breeding area (i.e. pond cluster). A recent review of amphibian movement distances shows a strong positive relationship between the distances at which the sites searched for recaptures were situated and the movement distance of amphibians (Smith & Green 2005).

Females tended to move to larger distances in the years with more precipitation, whereas no similar pattern was apparent in males. It is possible that females explore more ponds for reproduction in rainy periods to assess their quality for reproduction. The increased moisture in the terrestrial habitats also may favour such movements. The reproductive failure may be higher in females than in males because females have larger reproductive effort than males (the eggs are more costly to produce than sperm [Halliday 1994]). In rainy years more habitats become available (Hartel et al. 2007b) and there may be a competition between the reproductive females to (firstly) exploit these ponds. I have repeatedly observed that female Yellow Bellied Toads in this population avoid breeding in the same ponds where the conspecific larvae or other species, especially *Rana temporaria* and *R. dalmatina*, are present in high densities, most probably because of the opportunistic predation by the other anuran larvae. Predation of *B. variegata* eggs by *R. dalmatina* larvae was experimentally shown by Heusser et al. (2002).

Experimental studies on Yellow Bellied Toad larvae originating from this population indicate that the larval mortality is large in crowded conditions (even when the per capita food rate is kept constant) and in those low density trials when a larger conspecific was present (Hartel 2007). Jasienski (1988) compared the growth and development of sibling and nonsibling *B. variegata* larvae under high density conditions and found a negative effect of the larger nonsibling tadpoles. These results indicate that those ponds that are already occupied by larvae (conspecific or not) are of low quality for this species. Although a preference for intermediate-long duration ponds for breeding was observed in this population, the efficient location and exploitation of the newly created ephemeral? ponds for reproduction was also observed in this species (Barandun & Reyer 1998) and this population (Hartel et al. 2007a). This is possible using intense movement activities (this study).

The movement distance was positively related to female body size. In amphibians there is a general correlation between the body size of the females and fecundity (the number of eggs produced) (Duellmann & Trueb 1986). It is possible that larger (older) more experienced females are more efficient in locating new ponds than younger ones. Ponsèro & Joly (1998) found a significant positive relationship between the migration distance and female body size in *Rana dalmatina*, larger females being able to reach breeding ponds at further distance from the forest than the smaller females. They assumed that by this behavior, large females decrease competition between larvae, thus increase their reproductive success, if deposit at larger distance from the forest where the the smaller sized females cannot reach.

In conclusion, the Yellow Bellied Toads intensively move between ponds, and their movement, especially those of the females, is strongly influenced by precipitations. The efficient conservation of this species requires the protection of groups of interconnected ponds (i.e. the patchy population approach, *sensu* Petranka et al. 2006). The maintenance of an adequate density of ponds will allow the choose of the optimal ponds for breeding and decreasing the isolation by distance between the aquatic habitats will facilite the toads movements through the landscape. The pond based recaptures only, may underestimate the real dispersal distances in amphibians, thus, I suggest more studies to explore the amphibians movement distance in various terrestrial habitats. As the Yellow Bellied Toad is an important Habitat Directive species, and a large part of the middle section of the Târnava Mare basin was proposed as Natura 2000 site, our research in this area aims to locate, protect, and if needed, restore these wetlands. The future of this population is not sure: in 2007 two major wetlands were partially drained (ponds 12 and g2) and around one hectar of forest was cleared for gas extraction activities. This situation is unfortunate because the main part of the documentation for creating this Natura 2000 (i.e. the understanding of the spatio-temporal dynamic of the habitat use) site was based on the studies on this population of Yellow Bellied Toads (Hartel *unpublished report*).

**Acknowledgements**

Here I thank to many colleagues and pupils for their help in the fieldwork. Thanks to Dr. Günter Gollmann, Dr. Gyöngyvér Mara, László Demeter and an anonimous reviewer for their critical observations on the manuscript and literature providing. Many thanks to Florica Vidreanu from the water station Albesti, for providing detailed data o the precipitations.

**References**

Adler, F.R., Nuernberger, B. (1994): Persistence in patchy irregular landscapes. Theoretical Population Biology 45: 41-75.

Barandun, J. (1992): Reproductive flexibility in *Bombina variegata* (Anura: Discoglossidae). In: Korsós Z. & Kiss Z. (eds), Proceedings of the 6th Ordinary General Meeting of the Societas Europaea Herpetologica 19-23 August 1991, Budapest, Hungary: 65-68.

Barandun, J., Reyer, H.U. (1997a): Reproductive ecology of *Bombina variegata*: characterisation of spawning ponds. Amphibia-Reptilia 18: 143-154.

Barandun, J., Reyer, H.U. (1997b): Reproductive ecology of *Bombina variegata*: development of eggs and larvae. Journal of Herpetology 31: 107-110.

Barandun, J., Reyer, H.-U. (1998): Reproductive ecology of *Bombina variegata*: habitat use. Copeia 2: 407-500.

Beshkov, V.A., Jameson, D.L. (1980): Movement and Abundance of the Yellow-Bellied Toad *Bombina variegata*. Herpetologica 36: 365-370.

Bowler, D.E., Benton, T.G. (2005): Causes and consequences of animal dispersal strategies: relating individual behavior to spatial dynamics. Biological Review 80: 205–225.

Dall`Antonia, P., Sinsch, U. (2001): In search of water: orientation behaviour of dehydrated natterjack toads, *Bufo calamita*. Animal Behaviour 61: 617-629.

Diffendorfer, J. E. (1998): Testing models of source sink dynamics and balanced dispersal. Oikos 81: 417-433.

Duellman, W.E., Trueb, L. (1986): The Biology of Amphibians. Baltimore and London. John Hopkins Press.

Feder, E.,M., Burggren, W.W. (1992): Environmental Physiology of the Amphibians. Univ. of Chicago Press, Chicago and London.

Gill, D.E. (1978): The metapopulation ecology of the red spotted newt, *Notophtalmus viridescens* (Rafinesque). Ecological Monographs 48: 145-166.

Gollmann, G., Gollmann, B. (2000): Wiederfangstudie an einer Gelbbauchunken population: Überlebensraten und Ausbreitung. Beitr. Ökol. 4: 75-82.

Gollmann, B., Gollmann, G., Miesler, M. (2000): Habitatnutzung und Wanderungen in einer Gelbbauchunken-Population (*Bombina v.*

*variegata*). Zeitschrift für Feldherpetologie 7: 1-16.

Gollmann, G., Gollmann, B. (2005): Postmetamorphic growth and movements in Yellow Bellied Toads, *Bombina variegata*: approaching life path analysis. In: Ananjeva, N., Tsinenko, O. (Eds.), Herpetologia Petropolitana. Proc. of the 12th Ord. Gen.Meeting Soc. Eur. Herpetol., August 12– 16, 2003, S.E.H., St. Petersburg, pp. 143-145.

Gros, A., Poethke, H.J., Hovestadt, T. (2006): Evolution of local adaptations in dispersal strategies. Oikos 114: 544-552.

Halliday, T.R. (1994): Sex and evolution. In. Behaviour and Evolution (Slater, P.J.B. and T.R. Halliday eds.). Cambridge University Pres. 150 – 192.

Hansson, L.H. (1991): Dispersal and connectivity in metapopulations. Biological Journal of Linnean Society 42: 89-103. In: Gilpin, M. & Hanski, I. (Eds.): Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press.

Hartel, T. (2007): An experimental study on the abundance effect on tadpole growth, mortality and metamorphosis in *Bombina variegata*. Biota - Journal of Biology and Ecology 6: 27-34.

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

Hartel, T., Nemes, Sz. (2006): Toe clipping and body condition at yellow belied toads, *Bombina variageta*. Acta Zoologica Academiae Scientiarum Hungaricae 52: 359-366.

Hartel, T., Nemes, Sz., Mara, Gy. (2007a). Spatial and temporal dynamic of pond use by a hybrid fire-bellied toad population: the importance of pond availability and duration. Acta Zoologica Lituanica 17: 56-63.

Hartel, T., Öllerer, K., Nemes, Sz. (2007b). Critical elements for biologically based management plans for amphibians in the middle section of the Târnava Mare basin. Acta Scientiarum Transylvanica 15: 109-132.

Hartel, T., Moga, C.I., Öllerer, K., Sas, I., Demeter, L., Rusti, D., Balog, A. (2008): A Proposal towards the incorporation of spatial heterogeneity into animal distribution studies in Romanian landscapes. North-Western Journal of Zoology, Online first.

Hazzell, D., Osborne, W., Lindenmayer, D. (2003): Impact of post-European stream change on frog habitat: southeastern Australia. Biodiversity and Conservation 12: 301-320.

Hero, J.M. (1989): A simple code for toe clipping anurans. Herpetological Review 20: 66-69.

Heusser, H., Lippuner, M., Schmidt, B. (2002): Laichfressen durch Kaulquappen des Springfroschs (*Rana dalmatina*) und syntopes Vorkommen mit andern Anuren. Zeitschrift für Feldherpetologie 9: 75

Hopey, M.E., Petranka, J.W. (1994): Restriction of wood frogs to fish-free habitats: how important is adult choice versus direct predation? Copeia 1994: 1023-1025.

Jasienski, M. (1988): Kinship ecology of competition – size hierarchies in kin and nonkin laboratory cohorts of tadpoles. Oecologia 77: 407-413.

Joly, P., Miaud, C. (1993): How does a newt find its pond? The role of chemical cues in migrating newts (*Triturus alpestris*). Ethology Ecology & Evolution 5: 447-455.

Laurila, A., Aho, T. (1997): Do Female Common Frogs Choose Their Breeding Habitat to Avoid Predation on Tadpoles? Oikos 78: 585-591.

Matthysen, E. (2005): Density dependent dispersal in birds and mammals. Ecography 28: 403-416.

Marchand, M. (1993): Untersuchungen zur Pionierbesiedlung terrestrischer und limnischer Habitate eines Bodenabbaugebietes im südlichen Wesertal mit besonderer Berücksichtigung der Biologie und Ökologie der Gelbbauchunke, *Bombina v. variegata*, Linnaeus 1758. Univ. Diss. Göttingen.

Marsh, D.M., P.C. Trenham (2001): Metapopulation dynamics and amphibian conservation. Conservation Biology 15: 40-49.

McCarthy, M. A. (1999): Effects of competition on natal dispersion distance. Ecological Modelling 114: 305-310.

Newman, R.A. (1992): Adaptive plasticity in amphibian metamorphosis. BioScience 42: 671 – 678.

Nuernberger, B. (2006): Local dynamics and dispersal in a structured population of the whirligig beetle *Dineutus assimilis*. Oecologia 106: 325-366.

Petranka, J.W., Hayes, L.J. (1998): Chemically mediated avoidance of a predatory odonate (*Anax junius*) by American toad (*Bufo americanus*) and wood frog (*Rana sylvatica*) tadpoles. Behavioural Ecology and Sociobiology 42: 263-271.

Petranka, J.W., Holbrook, C.T. (2006): Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? Restoration Ecology 14: 404-411.

Ponsèro, A., Joly, P. (1998): Cluth size, egg survival and migration distance in the agile frog (*Rana dalmatina*) in a floodplain. Archiv für Hydrobiologie 142: 343-352.

Pulliam, H. R., Danielson, B. J. (1991): Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137: 50-66

Roff, D.A. (1975): Population stability and the evolution of dispersal in heterogeneous environment. Oecologia 19: 217-237.

Semlitsch, R.D. (2008): Differentiating Migration and Dispersal Processes for Pond-Breeding Amphibians. Journal of Wildlife Management 72: 260-267.

Semlitsch, R.D., Bodie, J.R. (1998): Are small, isolated wetlands expendable? Conservation Biology 12: 1129-1133.

Sinsch, U. (1991): Mini review: the orientation behaviour of amphibians. Herpetological Journal 1: 541-544.

Sinsch, U. (1992): Structure and dynamic of a natterjack toad metapopulation (*Bufo calamita*). Oecologia 90: 489-499.

Smith, M.A., Green, D.M. (2005): Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 38: 110-128.

Wellborn, G.A., Skelly, D.K., Werner, E.E. (1996): Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecologycal and Systematical Research 27: 337-363.

Wilbur, H.M. (1980): Complex life cycles. Annual Review of Ecologycal and Systematical Research 11: 67-93.

Wilbur, H.M., Collins, J.P. (1973): Ecological aspects of amphibian metamorphosis. Science 182: 1305 – 1314.

*Submitted: 01 March 2008*
*/ Accepted: 11 April 2008*