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Spring migration rates and community structure of amphibians breeding in an old and newly established midfield ponds

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Abstract. We studied the amphibian breeding migration into an old established (the beginning of the 1990s) pond and a new one (2007), using drift fences in 2008–2011. The two ponds were located at a distance of about 0.5 km from one another in a post-agricultural landscape in the Mazurian Lakeland, north-eastern Poland. We examined the community structure and migration rates of adults and juveniles. The amphibian breeding communities were similar in the two ponds in each year. The moor frog *Rana arvalis* was the most common species and comprised between 35 and 55 % of all adult amphibians migrating to both ponds. The new pond was colonized by adult amphibians in the first spring after its creation. In the second year, the amphibian migration rates doubled in the new pond and remained stable over the next two years. However, during the entire period of the study the old pond was a more attractive spawning site than the new pond, when measured by the number of migrating individuals of all recorded species. Despite some annual variation, there were no significant differences between the ponds in terms of the sex structure, mean body mass or migration timing of the predominant amphibian species. The most probable explanation for the observed differences in the rates of migration is breeding site fidelity.

Key words: pond fidelity, colonization, anurans, newts

Introduction

Both small midfield ponds of natural origin and man-made ponds can support rich communities of animals, including amphibians (Williams et al. 2004, Scheffer et al. 2006, Davies et al. 2008). In the agricultural landscape, changes in land use may have a substantial negative impact on the abundance of small water-bodies and may lead to reductions in amphibian species richness and population numbers (Hartel et al. 2009a, Curado et al. 2011). While pond losses in agricultural landscapes and the consequences for biodiversity are well recognized, the effects of pond restoration on amphibian populations are less known but they are receiving increasing attention, especially in the context of protection of amphibians (e.g. Schlupp & Podloucky 1994, Lehtinen & Galatowitsch 2001, Pechmann et al. 2001, Rannap et al. 2009, Smith & Sutherland 2014). Colonization of newly created water-bodies by amphibians is a complex process that is related to their attractiveness as breeding sites, their connectivity with other ponds, the quality of adjoining terrestrial habitats and the condition and dynamics of amphibian populations inhabiting the

surrounding areas (Banks & Beebee 1987, Lehtinen & Galatowitsch 2001, Marsh & Trenham 2001). The attractiveness of ponds as amphibian breeding sites also depends on many variables including pond size, water depth, hydroperiod, pH, temperature, vegetation cover, and numbers of competitors and predators (Beja & Alcazar 2003, Denoël & Lehmann 2006). Furthermore, particular amphibian species have defined preferences for water-bodies of different successional stages (Semlitsch 2008).

The landscape of the Mazurian Lakeland in north-eastern Poland is characterized by a high density of small inland water-bodies (Solarzski & Nowicki 1990). During the 20th century, the number of small ponds in this region was decreasing, following the tendency characteristic for many European agricultural areas (Curado et al. 2011). However, since the 1990s the reverse trend is now being observed in some places. After the collapse of numerous state farms established in the communist period, large areas of farmland in the Mazurian Lakeland have been abandoned, and as fallows they have undergone secondary succession. Drainage systems, which mediated the outflow of

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water from fields, meadows and pastures, were no longer maintained, so the level of the ground water table increased and many previously drained marshes and small water-bodies started to recover. This process was also supported by the activity of the increasing beaver (*Castor fiber*) population. As a consequence of these processes, many small inland water-bodies distributed among fallows have developed as excellent breeding sites for various amphibian species. The main objectives of this study were (1) to identify breeding communities of amphibians migrating to ponds of different age, (2) to compare the intensity of amphibian migrations to an old and a newly created pond, and (3) to analyze year-to-year variability in body mass, sex ratio and in ratio of adults vs. juveniles of migrating individuals of selected amphibian species.

Material and Methods

Field studies were conducted in the central part of the Mazurian Lakeland, north-eastern Poland, in the district of Mikołajki. The study area extends along the eastern bank of the Biosphere Reserve “Lake Łuknajno” (53°49’ N, 21°38’ E) and includes over 2 km² of fallows, which were cultivated fields until 1991. In the process of natural secondary plant succession, the abandoned fields were initially overgrown with grasses and herbs, and later also with shrubs, mainly pear *Pyrus communis*, dog rose *Rosa canina* and common hawthorn *Crataegus monogyna*. The study area is adjacent to a large mixed-pine forest to the east. The two large ponds were selected to study amphibian migrations to their breeding sites: pond A and pond B, separated by a distance of 550 m (Fig. 1). There are several other small water bodies in the study area, which attract amphibians during the spawning season and which could influence migration rates to ponds A and B. Both ponds are of natural origin, i.e. they were not created by humans, but were formed in the postglacial landscape in depressions between sandy hills. However, drainage and land reclamation during the period when the fields were cultivated, caused the ponds to dry up. After blocking the water outflow from the ponds to the nearby Lake Łuknajno, both of them recovered: pond A at the beginning of the 1990s and pond B in 2007, when the last working underground drain-pipe was blocked. Therefore, at the beginning of the study, pond A was at least 15 years old, whereas pond B had just been filled. The ponds also differ in shape, size, shoreline length and depth (Table 1). They are overgrown by similar plant communities, but their relative proportions and range

vary significantly. Pond A is extensively overgrown by common reed *Phragmites australis* and lesser bulrush *Typha angustifolia*, and open water covers less than 1 % of the entire pond area. In contrast, pond B has a large open water area (48 %) and plants grow mainly along the shoreline (plant cover estimated in 2011). Water fluctuations were recorded each year during the study, but both ponds are deep enough to sustain a water level sufficient for spring breeding of amphibians. Neither pond dries out totally in summer and though they both freeze in winter, the bottom water layers remain unfrozen in the deeper parts. No fish were recorded in either of the ponds.

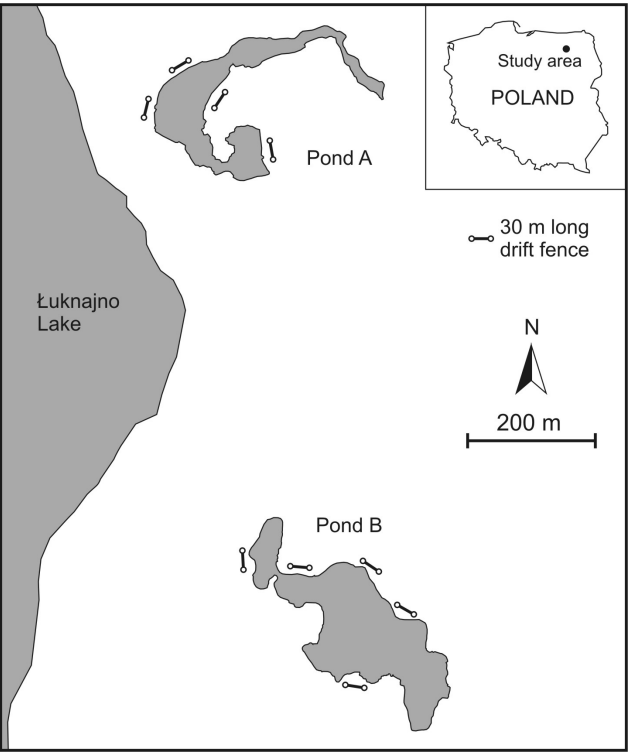


Fig. 1. Study area in the Mazurian Lakeland, north-eastern Poland.

Table 1. Physical and chemical parameters of the studied ponds (measurements taken in 2010).

	Pond A	Pond B
Area [ha]	2.96	6.58
Shoreline length [m]	1542	1966
Max. depth [cm]	40	104
Mean depth [cm]	29	64
pH	7.1	7.3
PO ₄ ³⁻ [mg/l]	0.33	0.43
NH ₄ ⁺ [mg/l]	0.79	1.11
NO ₃ ⁻ [mg/l]	0.20	0.22

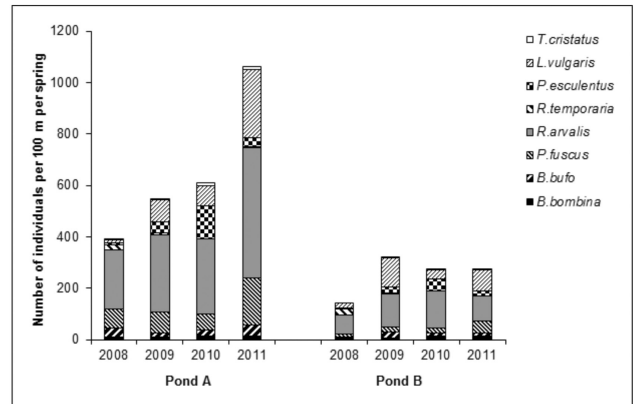
The overall abandonment of the agricultural practices in the past two decades resulted in the formation of

optimal terrestrial habitats for amphibians. The nearby mixed-pine forest is exploited extensively, but the patches of alderwood that extend along the lake are protected. Human activity is low and settlements in the vicinity of the study area (joined only by country roads) are small and dispersed.

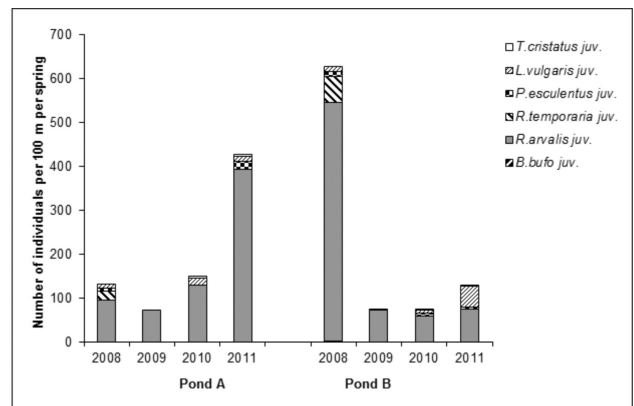
Data were collected during four consecutive years (2008-2011). Amphibian migrations were recorded from about the 10th of March to the 2nd of May each year. To monitor amphibian movements, 0.5-m-high plastic drift fences were constructed along the shoreline of each pond. Four 30-m-long fences were placed along the edge of pond A (total length 120 m, 8 % of the pond perimeter), and five 30-m-long fences were placed along the edge of pond B (total length 150 m, 8 % of the pond perimeter). These drift fences were distributed around the ponds (Fig. 1). Water-filled buckets were buried at the end of each fence to function as pitfall traps. During the spring study period in each year, the pond sites were visited every day if possible, but in some years there were several instances of intervals of 2-3 days between visits. Due to the different total lengths of the drift fences at ponds A and B, migration rates for each spring study period were expressed as the number of individuals captured per 100 m of fence.

Amphibians trapped in the buckets were identified (three frog species *Pelophylax lessonae*, *P. ridibundus* and *P. esculentus* were not distinguished and were treated as a single group – *Pelophylax esculentus* complex), counted, sexed, weighed (except the smooth newt *Lissotriton vulgaris*; incidentally some individuals belonging to other species were also not weighed) and released into the ponds. All moor frogs *Rana arvalis* and *Pelophylax esculentus* complex individuals weighing less than 6 g, common frogs *Rana temporaria* weighing less than 8 g, and common toads *Bufo bufo* weighing less than 10 g were classified as juveniles. The weight limits used to classify individuals as juveniles were set at the level that excluded incorporating to this age group subadults and small adults, and were based on morphological parameters given by Juszczuk (1987).

The sign test was used to compare the amphibian community at both ponds. Variation in migration rates of adult amphibians to ponds A and B in the consecutive years was assessed with Principal Component Analysis (PCA, length of gradient 0.766), with species arrows pointing in the direction of steepest increase of values for the corresponding species (CANOCO for Windows, Version 4.5) (ter Braak & Smilauer 1998).



A



B

Fig. 2. Migration rates of adult (A) and juvenile (B) amphibians to ponds A and B in years 2008-2011, expressed as the number of individuals captured per 100 m of drift fence during the spring sampling period.

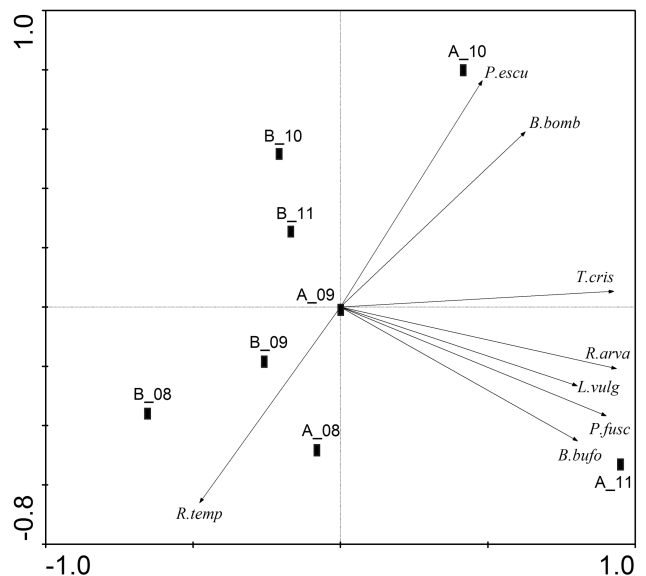


Fig. 3. Variation in the migration rates of adult amphibians to ponds A and B in years 2008-2011, calculated as a number of individuals captured per 100 m of drift fence during the spring sampling period. Principal Component Analysis, $\lambda_1 = 0.588$; $\lambda_2 = 0.228$; $\lambda_3 = 0.092$; $\lambda_4 = 0.049$.

Annual sex ratios of the predominant species were compared between ponds A and B with sign test, in which ratios for the same year were treated as dependent pairs (STATISTICA 10). Sign test was chosen because of the small number of compared pairs (four for each species). After analysis with Shapiro-Wilk test for normality, differences in body mass of adult amphibians migrating to the pond A and B were assessed with Kruskal-Wallis one-way analysis of variance (STATISTICA 10). This analysis was performed on the pooled data for the whole study period. Analyses of body mass for males and females were performed separately.

were captured: 4636 adults belonging to eight species (*Bombina bombina*, *Pelobates fuscus*, *Bufo bufo*, *Rana arvalis*, *R. temporaria*, *Pelophylax esculentus*, *Lissotriton vulgaris*, *Triturus cristatus*) and 2297 juveniles belonging to six species (juveniles of fire-bellied toad *B. bombina* and spadefoot *P. fuscus* were not recorded). The number of amphibians captured per year varied from 1330 in 2009 to 2395 in 2011. More adults were captured at pond A (67.5 % of all adults) and more juveniles at pond B (59.0 % of all juveniles). The most numerous species in the study area was the moor frog, which comprised 48.6 % of adult amphibians and 85.2 % of juveniles. The rarest

Table 2. Percentage occurrence of amphibian species migrating to ponds A and B in the spring sampling periods in years 2008-2011.

Adults	2008		2009		2010		2011	
	Pond A	Pond B	Pond A	Pond B	Pond A	Pond B	Pond A	Pond B
<i>B. bombina</i>	2.6	3.3	1.5	1.5	2.5	4.9	1.2	4.4
<i>P. fuscus</i>	19.2	7.0	15.2	7.0	10.4	7.2	17.1	17.0
<i>B. bufo</i>	8.7	4.7	3.1	7.2	3.7	4.7	4.2	4.9
<i>R. arvalis</i>	58.4	52.3	54.9	40.0	47.9	53.1	47.8	35.2
<i>R. temporaria</i>	5.1	16.4	0.9	1.5	0	0.5	0.4	0.5
<i>P. esculentus</i>	2.1	3.7	8.4	7.0	20.9	16.8	3.3	7.3
<i>L. vulgaris</i>	2.8	12.6	15.7	35.8	12.7	12.6	24.7	30.1
<i>T. cristatus</i>	1.1	0	0.3	0.2	1.9	0.3	1.3	0.7
N	469	214	656	475	731	405	1274	412
Juveniles								
<i>B. bufo</i>	0	0.3	0	1.8	0.6	0.9	0	0
<i>R. arvalis</i>	73.0	86.9	100	96.4	85.6	80.9	91.8	58.0
<i>R. temporaria</i>	14.5	9.2	0	0	0	0	0.2	0
<i>P. esculentus</i>	5.7	1.9	0	1.8	0	8.2	3.9	4.1
<i>L. vulgaris</i>	6.9	1.7	0	0	11.7	9.1	3.1	36.9
<i>T. cristatus</i>	0	0.0	0	0	2.2	0.9	1.0	1.0
N	159	940	88	111	180	110	514	195

Table 3. Comparison of medians and ranges of body masses of particular species migrating to ponds A and B in years 2008-2011 (p values calculated with Kruskal-Wallis test). M – male, F – female.

Species	Pond A			Pond B			p
	N	median	min-max	N	median	min-max	
<i>B. bufo</i> M	49	24	13-41	35	24	18-44	0.7503
<i>B. bufo</i> F	85	48	17-87	29	44	22-60	0.0436
<i>P. fuscus</i> M	280	8	5-12	94	8	5-11	0.9753
<i>P. fuscus</i> F	171	11	5-26	45	13	7-19	0.0122
<i>R. arvalis</i> M	823	12	6-23	238	12	7-20	0.0563
<i>R. arvalis</i> F	746	9	6-20	382	9	6-18	0.0908
<i>P. esculentus</i> M	145	13	6-27	79	15	8-41	0.0000
<i>P. esculentus</i> F	62	17	7-60	52	18.5	9-37	0.0562

Results

Amphibian community structure

During the study period, a total of 6933 amphibians

was the crested newt *T. cristatus* (42 captures; 0.9 % of adult amphibians). In each year, all amphibian species recorded in the study area were captured at

both ponds, except for the crested newt, which was not found at the newly created pond B in the first year of the study.

The structure of the adult amphibian community at both ponds was similar (sign test, for all species and years $p > 0.05$) and despite yearly fluctuations in the numbers of migrating amphibians, the proportions of particular species in each community were stable during the whole study period (Table 2). Each year the moor frog predominated, representing from 47.8 to 58.4 % of the amphibian community at pond A, and from 35.2 to 53.1 % at pond B. Similar percentage occurrences of most species were observed at the two ponds, with the most pronounced differences seen in the smooth newt, which was more numerous at pond B, and the spadefoot and the moor frog, which were more numerous at pond A. The small year-to-year changes in the proportions of most species had the same pattern; we did not observe different trends for the two ponds. Moor frogs were always predominant

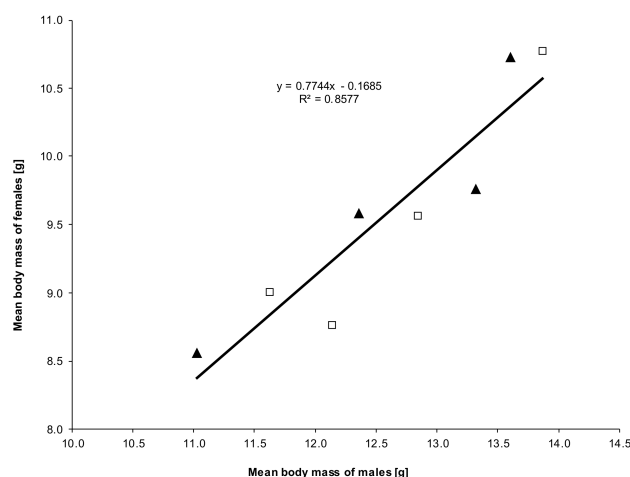


Fig. 4. Correlation between the mean body masses of moor frog males and females in particular years of the study at ponds A (white squares) and B (black triangles).

Table 4. Mean body masses of moor frog and spadefoot males and females in consecutive years of the study. SD in brackets. M – male, F – female.

Pond/year	<i>R. arvalis</i>	<i>R. arvalis</i>	<i>P. fuscus</i>	<i>P. fuscus</i>
	M	F	M	F
A/2008	13.9 (2.9)	10.8 (2.9)	8.6 (1.5)	12.8 (3.4)
A/2009	12.1 (2.9)	8.8 (2.4)	7.3 (1.7)	11.4 (4.0)
A/2010	11.6 (2.7)	9.0 (2.0)	8.0 (1.4)	12.7 (4.3)
A/2011	12.9 (2.8)	9.6 (2.7)	8.1 (1.3)	11.8 (2.3)
B/2008	13.3 (3.0)	9.8 (2.8)	8.8 (2.1)	13.8 (1.9)
B/2009	11.0 (2.3)	8.6 (2.2)	7.6 (1.4)	13.2 (3.9)
B/2010	12.4 (2.4)	9.6 (1.9)	7.7 (1.5)	11.0 (1.7)
B/2011	13.6 (2.9)	10.7 (3.1)	8.3 (1.2)	12.4 (1.6)

among juvenile amphibians; their lowest percentage occurrence (59 % of all juvenile specimens) was recorded at pond B in 2011, and the highest (100 % of all juvenile specimens) at pond A in 2009 (Table 2).

Amphibian migration rates

The overall migration rates of all adult amphibians, calculated for both ponds jointly, increased from 2008 to 2011 (533.5 amphibians in 2008 vs. 1336.3 amphibians in 2011 per 100 m drift fence). The migration rates of adult amphibians differed between years and ponds, but they were higher at pond A than at pond B every year (from 1.7-fold higher in 2009 to 3.9-fold higher in 2011) (Fig. 2). The number of migrating adults at pond A increased between the years 2008 to 2011. At pond B it was the lowest in 2008, increased in 2009 and was stable in the following years. In general, differences between the rates of migration of all amphibian species to pond A and to pond B were highest in years 2010 and 2011 (Fig. 3). Points representing migration rates for ponds A and B in consecutive years are dispersed on the diagram, yet records for pond A are separated from those for pond B by a diagonal. Points representing records for ponds A and B for the same year are relatively close to each other (except in 2011), indicating seasonal tendencies in amphibian migration rates in the study area.

The migration rates of juveniles were 4.9-fold higher at pond B in 2008 than at pond A, similar for both ponds in 2009, and higher at pond A in 2010 and 2011 (2.1-fold and 3.3-fold, respectively) (Fig. 2). The number of juveniles captured at pond B was remarkably high in spring 2008 (627 individuals per 100 m of drift fence), but in the following three years of the study, the rates of spring migration to this pond declined to 73-130 individuals per 100 m. In contrast, the highest migration rate of juveniles at pond A (428 individuals per 100 m of drift fence) was recorded in the final year of the study.

Amphibian sex ratio and body mass

At both ponds, the sex ratios of the three predominant amphibian species (*R. arvalis*, *P. fuscus* and *L. vulgaris*) varied from year to year (due to the small sample size, sex ratio was not calculated for other species). The sex ratio (F/M) of the moor frog ranged from 0.79 to 1.08 at pond A, and from 1.21 to 2.54 at pond B. In each year, moor frog females comprised a higher proportion of adults migrating to pond B than to pond A. However, comparison between the two ponds did not show any significant differences in sex ratio ($p = 0.1336$, in inter-pond comparisons

by the sign test for sex ratio). The sex ratio (F/M) of spadefoot ranged from 0.34 to 1.09 at pond A and from 0.12 to 2.75 at pond B. Only in 2008 were spadefoot females more numerous than males (at both ponds), whereas in subsequent years, males predominated. No significant differences in the sex ratio of this species between the two ponds were recorded ($p = 0.6171$, in inter-pond comparisons by the sign test for sex ratio). In each year at both ponds, smooth newt females were more numerous than males. In the years 2009–2011 the sex ratio (F/M) of this species ranged from 2.10 to 3.33 at pond A and from 1.32 to 2.02 at pond B (no sex ratio was calculated for 2008 because the number of captured newts was very low in this year). Comparison of the sex ratios in the two ponds did not show any significant differences between them ($p = 0.6171$, in inter-pond comparisons by the sign test for sex ratio).

We recorded significant differences in the mean body masses (pooled data for the whole study period) of three anuran species/sexes migrating to ponds A and B (Table 3). On average, common toad females were heavier at pond A than at pond B. In contrast, spadefoot females and *R. esculenta* complex males were significantly heavier at pond B than at pond A. No statistically significant differences in the mean body masses of both sexes of the moor frog and other species were recorded between the two ponds. Moor frog and spadefoot males and females at both ponds displayed annual variation in their mean body mass (Table 4). There was a significant correlation between the mean body masses of moor frog males and females in certain years of the study at ponds A and B (Fig. 4), but no such correlations were found for the other species.

Discussion

The age of breeding ponds seems to be important for amphibians. The study of Laan & Verboom (1990) proved that pond age is the best predictor of species number in newly created ponds. Also Stevens et al. (2006) found that younger beaver ponds used as amphibian breeding sites had a lower species richness than older ones. The study of Pechmann et al. (2001) showed that differences in the amphibian communities among created ponds and between the ponds and a reference wetland, were likely to be related to the age of these breeding sites, their hydrologic regime, size, vegetation and surrounding terrestrial habitats, but also to the limited availability of colonists of some species. In contrast, Dalbeck & Weinberg (2009) did not find evidence supporting

the notion that younger ponds have a lower species richness. Thus, the number of amphibian species breeding in a certain pond may depend more on the age of the amphibian community than on the age of the pond. However, other studies that did not directly analyze the influence of pond age, have indicated that species richness of amphibian breeding communities in a certain area depends on pond features such as permanence, hydroperiod, vegetation cover, depth and area (Snodgrass et al. 2000, Beja & Alcazar 2003, Jakob et al. 2003, Richter-Boix et al. 2007, Hartel et al. 2009a).

The amphibian community in the Mazurian Lakeland comprises 13 species (including three species of the *Pelophylax esculentus* complex). Two of them, *Pseudepidalea viridis* and *Epidalea calamita*, were not recorded in the study site and the tree frog *Hyla arborea* inhabited the area, but could not be captured using drift fences and pitfall traps. The members of the other seven species and the *Pelophylax esculentus* complex were captured in each year of this study. Therefore, all species known to live in the study area, and which could be effectively captured, were recorded at both ponds, and the structures of species dominance were very similar, so pond age did not influence the species richness. The studied ponds were relatively closely situated to each other (550 m). This distance is well within the migration and dispersal distances of the European amphibians (Kovář et al. 2009) and we suspect that the individual exchange between these ponds is high, and the two ponds are used by the same breeding assemblage. Therefore, the populations of amphibian species in the study area could be defined as local populations consisting of individuals that use cluster of ponds in a relatively small area, and which constitute a single breeding unit (Semlitsch 2008). The lack of isolation of pond A and pond B, neither by distance nor by any habitat barriers, is of particular importance, because breeding pond isolation may have significant effects on amphibians. Negative correlations between pond isolation and their use by amphibians have been identified in several studies (Laan & Verboom 1990, Sjögren 1991, Vos & Stumpel 1995, Marsh et al. 1999, Lehtinen & Galatowitsch 2001).

Throughout the whole study period, the rates of migration to pond A were significantly higher than to pond B. This suggests that the old pond was a more attractive breeding site than the newly created one. Plant succession in newly created ponds leads to increase in the area covered by reedswamp communities (Kłosowski & Jabłońska 2009), which

should be favourable for breeding amphibians (Hartel et al. 2009b). However, in our study the numbers of adult amphibians migrating to pond B remained low and stable in the consecutive years of the study. Other factors that might have resulted in increased migration rates to the old pond compared with the new one were the higher densities of over-wintering amphibians in the vicinity of the former and the better connections with suitable hibernation sites. In spring, amphibians move directly to the breeding ponds from their terrestrial habitats. These movements are non-random and certain directions are favoured (Dodd & Cade 1998). Therefore, the location of good quality terrestrial habitats in the proximity of a breeding pond may significantly affect the direction and rate of spring migration. Moreover, amphibians tend to migrate and aggregate in the pond where the number of spawning individuals is higher (Gamble et al. 2007). However, the most probable explanation for the recorded differences in the migration rates to both ponds is the fidelity of amphibians to the breeding sites. Adult amphibians display the ability to move to their natal ponds or to those in which they have bred before. Some amphibian species show high pond fidelity (Berven & Grudzien 1990, Reading et al. 1991, Hels 2002, Smith & Green 2006, Matthews & Preisler 2010), while others move between neighbouring breeding sites (Petranka & Holbrook 2004). Smith & Green (2005), after reviewing available data, concluded that the majority of amphibian species do not move further than 1 km, only 5 % are capable of movements of more than 10 km. Kovář et al. (2009) estimated the spring migration distances for the anurans (*B. bombina*, *B. bufo*, *R. arvalis* and *R. temporaria*) to be between 170-2214 m, and for the newts *L. vulgaris*, *T. cristatus* and *Ichthyosaura alpestris*, between 105-866 m. Jehle & Arntzen (2000) radio-tracked two newt species (*T. cristatus* and *T. marmoratus*) and found that the maximum migration distance did not exceed 150 m, and none of the individuals dispersed to other breeding sites. Despite the fact that the relationship between pond fidelity and survival or breeding success of amphibians is poorly understood, site fidelity is considered to have important ecological and evolutionary implications. In general, breeding site fidelity is thought to be advantageous for adults because individuals returning to the same pond may have higher survival rates and greater reproductive success compared with those that search for alternative and usually unknown breeding sites (Semlitsch 2008). However, Perret et al. (2003) found that annual survival rates in established alpine

newt population where individuals moved within pond system were significantly higher than annual survival rates in a population colonizing newly created ponds where newts did not display any local dispersal. Philopatry in amphibians may also have negative consequences, since maintaining site fidelity to disturbed and deteriorating breeding habitats can result in reproduction failure and population decline (Matthews & Preisler 2010).

In the temperate zone, seasonal migrations of adult pond-breeding amphibians from terrestrial habitats to aquatic breeding sites occur in the spring (reviewed by Russell et al. 2005). Spring migrations of adult amphibians are associated with local breeding populations that are restricted to terrestrial habitats surrounding one breeding site or a nearby cluster of ponds. Therefore, switching from one breeding pond to another may happen most frequently when a new pond is formed in close proximity to an existing pond and in an individual's migration path (Semlitsch 2008). For example, Reading et al. (1991) found that the degree of relocation of common toad individuals between ponds was negatively correlated with the distance separating the ponds and Rannap et al. (2009) showed that newly constructed ponds situated close to the source pond were colonized by crested newt and common spadefoot more quickly than more distant ponds.

The number of individuals of the various amphibian populations in our study area that were philopatric and how many changed breeding site remain open questions. Hels (2002), who studied a spadefoot population over a four-year period and analyzed the translocation of adults between five closely grouped ponds (maximum separation distance 575 m), found that only about 1 % of marked individuals changed pond during the study period. As we did not mark amphibian individuals during our study, it was not possible to determine breeding site fidelity, and we could not estimate the number of individuals of particular species changing from one pond to the other during the four year period. As pond A was an old pond in which amphibians had spawned for many years, it may have been treated as a source pond from which individuals could move to other ponds to find better breeding sites. However, we did not observe amphibian outflow from pond A to pond B as the number of amphibians migrating to the former did not decrease after the latter became a new breeding site. Therefore, there was no source-sink relationship between the old and the new ponds. On the contrary, there was a significant increase in the number of

amphibians migrating to pond A. The higher migration rates to the old pond might have resulted from the overall increase in the number of amphibians in the study area in the years 2008–2011. Indeed, we cannot exclude the possibility that some individuals that were breeding in pond A in the past migrated to pond B. However, it is also probable that most amphibians migrating to the newly created pond must have bred in some other, not very distant, breeding sites in the previous years.

According to the long-term studies of Pechmann et al. (2001), amphibian migrations to newly created ponds were very low in the first two years after their construction, increased in the third and fourth years and varied significantly in the following years. In general, the time needed for the colonization of a pond by amphibians increases with pond isolation (Marsh et al. 1999). It should be emphasized that in our study the new pond B was quickly recognized by amphibians as a possible spawning site. Adults of all species (except crested newt) migrated to this pond in the first year of its existence. The migration rates of adult amphibians to pond B increased over twofold in the second year after the pond was created, but no significant increase in migration was observed in the third and fourth years of the study, and the amphibian numbers even decreased slightly. Year-to-year variation in the number of amphibians migrating to a particular breeding pond may be significant (Pechmann et al. 2001) and it could result from the over-wintering survival, amphibian spring densities and the variation in the percentage of a population that successfully completes a migration. Several amphibian species exhibit migratory plasticity, and the decision to migrate to a certain pond is often influenced by environmental factors (Grayson & Wilbur 2009).

Year-to-year variations in the sex ratio and mean body mass of the predominant amphibian species were recorded in the study area. At the breeding sites, a male-biased sex ratio is typical for many amphibian species but among year variation in the sex ratio has been observed (Elmberg 1990, Friedl & Klump 1997, Loman & Madsen 2010). In the study area, male-biased sex ratio was well pronounced in spadefoot population, whereas in other predominating species, the moor frog and the smooth newt, females in most years comprised majority of adult individuals. However, in general, we did not observe any significant differences in variations in the sex ratio and mean body mass between two ponds (besides larger spadefoot females migrating to pond

B, but not every year). These findings suggest that the processes of colonizing the new pond did not involve any particular fractions of the amphibian populations. Sex and body mass did not determine the probability of breeding in a newly created breeding site. Despite the predictions that sex and body size may affect the mobility of migrating amphibians, sex- or body size-biased dispersal was not detected in several previous studies (Smith & Green 2006, Grayson & Wilbur 2009).

The migration rates and the community structure of juvenile amphibians that we observed were quite different from those of adults. At both ponds, juvenile moor frogs predominated significantly throughout the whole study period. In the first year of the study the migration of juvenile frogs to the newly created pond B was much higher than the migration of adults and it was also significantly higher than the rate of migration of juveniles to pond A. This result is consistent with the notion that juveniles are more likely to disperse to new sites than adults (Semlitsch 2008), although high pond philopatry has also been observed in juveniles of some species (Berven & Grudzien 1990, Reading et al. 1991). In general, it may be concluded that juvenile dispersal (characterized by large dispersal distances) and their relatively low philopatry compared with adults are essential for the landscape connectivity of amphibian populations (Cushman 2006). Juvenile amphibian movements have been described as a multi-phase process (Pittman et al. 2014). They represent more of a dispersal than directional migrations, and can last for several years until the juveniles achieve reproductive maturity and select a certain pond as their breeding site. The long distance dispersal of juvenile amphibians from their natal ponds is likely to be a random process, as there is no evidence that they have specialized perceptual abilities to locate new breeding sites (Rittenhouse & Semlitsch 2006, Semlitsch 2008). The initial juvenile movements differ from the targeted movements of adults toward the known locations of breeding sites (Pittman et al. 2014). For example, Rothermel (2004) found that emigrating salamanders did not respond to distant cues, but rather to microtopographic features. Therefore, breeding ponds appear to be found by dispersing juveniles primarily by chance and the probability of colonizing a new pond is likely to be a consequence of distance traveled, density of ponds in the area, the presence of habitat barriers and other landscape features (Rothermel & Semlitsch 2002).

This study enabled us to analyze migrations driven by demographic processes occurring over relatively

short time period, rather than amphibian dispersal at the metapopulation scale, which occurs over longer periods of time and involves multiple generations of amphibians (Semlitsch 2008). Despite some numerical changes, an old pond has represented an attractive amphibian breeding site in all years of the study and was a more attractive spawning site than the new pond, when measured by the number of migrating individuals of all recorded species. The amphibian species richness in both ponds remained unchanged and we saw no interannual turnover in the amphibian community, which is often a highly dynamic process dependent on many environmental factors including hydroperiod, pond area and connectivity with terrestrial

habitats (Werner et al. 2007). The new pond seems to have some potential for breeding amphibians but this potential is not yet utilized, because community of adults is not fully established there. Dataset from longer time period is needed to answer whether newly established pond might develop as such attractive breeding site as an old one.

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