

Does landscape and habitat limit the frogs *Rana arvalis* and *Rana temporaria* in agricultural landscapes? A field experiment

Jon Loman¹ and Björn Lardner

Department of Animal Ecology, Lund University, SE-223 62 Lund, Sweden

¹ Corresponding author; e-mail: jon.loman@zooekol.lu.se

Abstract

Frogs are often rare or absent from intensively farmed areas. Here we explore the possibility that the landscape and the quality of the terrestrial habitat are unsuitable for these populations. Spawn of *Rana arvalis* and *R. temporaria* was introduced into ponds in a south Swedish agricultural landscape in 2003 (eight ponds) and 2004 (ten ponds). Metamorphs emerged from nine (*R. a.*) and 12 (*R. t.*) of these. In years following the introduction, spawn was found in five (*R. a.*) and eight (*R. t.*) of these 18 ponds. The number of spawn clumps peaked two years after the introduction. Three or four years after the introduction, breeding persisted in only two of the ponds (where both species were breeding). One year later also these populations had also become extinct. In control ponds (ponds within 750 m of the introduction ponds), spawn of *R. temporaria* was occasionally found but there was no trend, nor any temporal peak in frequency or quantity of spawn in these ponds. There were calling males of both species already one year after the introduction at a few ponds, indicating an unusually early maturation for some individuals. We suggest that the terrestrial habitat in this region is not suitable for the continued presence of populations of *R. arvalis* and *R. temporaria*. This may be related to the habitat per se or to the isolation of the populations.

© Koninklijke Brill NV, Leiden, 2009

Key words

Anura, connectivity, farm land, growth, sexual maturity, terrestrial habitat.

Introduction

Agricultural landscapes containing arable land are in many regions the dominating habitat, having little resemblance to natural habitats. Few animal species have their main distribution in this kind of habitat and frog diversity is typically much lower in agricultural areas than in surrounding habitats (Bonin et al., 1997; Lehtinen et al., 1999; but see Gagné and Fahrig, 2007). Although this may be an effect of the habitat per se it is also important to recognize the structure of the surrounding habitat in a landscape when evaluating its effect on animal populations (Bennett et al., 2006).

Although areas with intensive agriculture are rarely optimal for amphibians (Gray and Smith, 2005), *Rana temporaria* L. (common frog) is occasionally found in the agricultural landscape of Scania, the southernmost province of Sweden (Loman, 2005). While *Rana arvalis* Nilsson (moor frog) is ecologically very similar to *R. temporaria* (Loman, 1979) and often breeds in the same ponds (Loman, 2005), it is very rarely found in the intensively farmed areas of this province (Berglund, 1976; Loman, 2005). But what are the key factors that make these and many other frog species occur so rarely, or not at all, in extreme agricultural landscapes?

In a previous study (Loman and Lardner, 2006) we investigated the suitability of the aquatic habitat that ponds in the south Swedish agricultural landscape offer tadpoles of these two regionally abundant frog species. While some of the study ponds were clearly unsuitable, mainly due to presence of decaying organic matter, many produced numerous and seemingly healthy metamorphs after introduction of frog spawn.

If the aquatic habitat is often suitable, why is *R. temporaria* rare and *R. arvalis* absent from this landscape? In this paper we address the possibility that this intensively cropped habitat limits frogs during their terrestrial life. Such limitation could be due either to local habitat quality, or to landscape level processes. Combined, our studies thus look at the habitat of these populations at three levels; breeding pond, terrestrial habitat and landscape (Denoel and Lehmann, 2006).

We do not try to estimate what aspect of the terrestrial habitat, or what landscape level processes, might be most important for the frogs in the agricultural landscape. We simply ask: Did the frogs that metamorphosed in ponds after our experimental introductions manage to survive to maturity and return to breed in the source pond or neighbouring ponds? If they did, there seems to be a possibility that the terrestrial habitat may not be prohibitively unsuitable for frog populations to persist. On the contrary, if we do not see any adult frogs returning to breed within a few years, the hypothesis that the terrestrial habitat sets a limit for frog populations in agricultural landscapes is supported.

To answer this question we surveyed the ponds where we had conducted experimental spawn introductions for adult frogs during the spring breeding season for up to 4 or 5 years after introduction. We also surveyed surrounding ponds to account for the fact that frogs might choose to migrate to ponds other than those where they stayed as tadpoles.

Methods

The study was performed in six different areas in western Scania, southern Sweden. These were all areas dominated by cropped fields. In Scania, *R. temporaria* only occasionally occurs in this habitat (Loman, 2005) while *R. arvalis* seems to be absent (Loman, 2008). In all six study areas, the “introduction ponds” plus all additional ponds within 750 m (“survey ponds”) were monitored for *Rana* spawn, starting

Table 1.

Overview of the occurrence of frogs in the study areas, both species (*R. arvalis* and *R. temporaria*) combined. Cell entries are the number of ponds in the respective area. Metamorphs = “yes” means that metamorphs emerged following the spawn introductions in 2003 or 2004, respectively. “Breeding” is the number of ponds where spawn was found in any of the study years (survey ponds) or in the years after spawn introduction (introduction ponds).

Area	Introd. year	Survey ponds			Introduction ponds			
		Breeding		Breeding in ponds:	Metamorphs		Breeding	Breeding in ponds:
		Never	Sometimes		None	Yes		
Härslöv	2003	3	1	Hars7	0	1	1	Hars1
Remmarlöv	2003	12	1	Rem6	1	3	3	Rem2, Rem7, Rem12
Rosenhäll	2003	7	1	Ros79 ^a	0	3	2	Ros1, Ros5
Borgeby	2004	3	2	Borg1, Borg2 ^a	2	1	1	Borg3
Igellösa	2004	7	2	Igel11 ^a , Igel8 ^a	1	2	1	Igel2
Svenstorp	2004	10	0		2	2	0	
Total		42	7		6	12	9	

^a These four survey ponds were situated on the 750 m border for inclusion as survey pond and spawn was found in these already before the introduction of spawn into the introduction ponds.

with the 2003 breeding season. The number of introduction ponds per study area varied from 1–4, with 4–13 survey ponds per area (table 1). A proximity of 750 m was chosen to produce a sample of ponds sufficient to characterize each study area with respect to frog occurrence. We do not imply that this is the limit to these frogs’ dispersal abilities.

Spawn introductions were made in 2003 (eight ponds) and 2004 (ten ponds). Spawn from both study species was placed in shallow water in the introduction ponds to mimic natural breeding sites of these species. Each pond received 20 spawn clumps from *R. temporaria* and another 20 from *R. arvalis*. Spawn of *R. temporaria* was collected from two (2003) and three (2004) ponds in central Scania. Spawn of *R. arvalis* was collected from the same number of ponds in the Revinge area, south central Scania. The choice of ponds was dictated by the availability of large breeding sites that could withstand the removal of large numbers of spawn clumps.

The introduction ponds were monitored for metamorphs at repeated visits in June and July of the year of spawn introduction (see Loman and Lardner, 2006 for details). Because the size, shape and shore structure differed among ponds, the number of metamorphs found give only a very crude index of the actual number of metamorphosing frogs.

Monitoring of breeding in all introduction and survey ponds continued until the breeding season of 2007. At this time any adult frogs originating from the introduced eggs were 3 or 4 years old, depending on study area. Unfortunately, four

non-introduced *R. temporaria* spawn clumps were laid and found in one Introduction pond (Hars1) in the year of introduction, after the spawn introduction was made. For the Härslöv area, conclusions are thus weakened for *R. temporaria* but the experiment is fully valid for *R. arvalis*. Ponds where spawn was found in 2007 were finally monitored also in 2008.

Results

With one exception (Hars1), no spawn was found in the introduction ponds in the year of spawn introduction or (for study areas with experiments starting only in 2004) in the year before (tables 1, 2). In the survey ponds, spawn of *R. temporaria* was found in four ponds (out of 49) in the year of introduction or before. All of these (Ros79, Borg2, Igel8, Igel11) were about 700 m from the closest introduction pond. One of these had a large breeding population of *R. temporaria*, with 60-300 clumps found during the years it was monitored. The other contained 2-6 clumps each (table 2). No *R. arvalis* spawn was found in introduction and survey ponds in the year of spawn introduction or before.

Metamorphs were found at 12 out of 18 introduction ponds. All 12 had *R. temporaria* metamorphs and nine also had *R. arvalis* metamorphs. In the other six ponds, the introductions thus failed already at the egg or tadpole stage. Already one year after introduction a few spawn clumps from *R. temporaria* were found in two introduction ponds (Ros1 and Borg3). In another two (Rem2: *R. temporaria* and *R. arvalis*; Hars1: *R. temporaria*) calling males were heard (table 2). Over the whole monitoring period, spawn from *R. arvalis* was found at five introduction ponds. Spawn from *R. temporaria* was found at 8 out of 12 ponds with metamorphs (table 1, table 2).

Although there were occasional observations of spawn in the year after introduction, most was found two years later. The amount of spawn and number of ponds with spawn dropped after that (table 2, fig. 1). In 2008, when only introduction ponds with spawn present in 2007 were surveyed, no *R. arvalis* spawn was found. *R. temporaria* spawn was still found in one pond (Hars1), this however was the introduction pond where *R. temporaria* spawn was found already at the start of the experiment. In the survey ponds, occasional spawn from *R. temporaria* (but none from *R. arvalis*) was found throughout the study but with no apparent effect from the timing of the introduction (fig. 1). Survey pond Ros79, on the 750 m border for inclusion, was an exception. It always contained much more than “occasional spawn” (table 2). However, also for this pond was it true that fluctuations in spawn number were not related to the year of introduction in Rosenhäll study area.

Thus, for *R. arvalis*, although neither type of pond contained spawn during the year of introduction or the year after, there were significantly more spawn clumps found in introduction ponds than in survey ponds two years after the introductions (Mann-Whitney *U*-test, $U = 280$, $P < 0.001$). In the year of introduction spawn from *R. temporaria* was found in one pond of each type and in the year after in two

Table 2.

Details for ponds where metamorphs and/or spawn clumps were found. Rows are individual ponds, sorted by (1) introduction year for study area, (2) pond type (introduction, survey) and (3) study area. Cell entries are number (metamorphs found or spawn clumps). 0* means that no spawn was found but calling males were heard. This was most likely to be heard (if present) in 2003 and 2004 when the ponds were surveyed by night at the time of expected toad *Bufo bufo* breeding. Only ponds were metamorphs or spawn (in addition to that introduced) was found are listed. The numbers of completely unsuccessful ponds are given in Table 1.

	<i>R. arvalis</i>										<i>R. temporaria</i>						Notes	
	Metamorphs			Spawn clumps							Metamorphs			Spawn clumps				
	2003	2004	2003	2004	2005	2006	2007	2008	2003	2004	2003	2004	2005	2006	2007	2008		
2003 introductions																		
<i>Intr. ponds:</i>																		
Hars 1	0	–	0	0	11	0	2	0	0	1	–	4	0*	12	0	6	9	a
Rem2	28	–	0	0*	7	4	6	0	0	3	–	0	0*	11	7	10	0	b, c
Rem12	15	–	0	0	7	0	0	–	–	10	–	0	0	5	0	0	–	d
Rem17	3	–	0	0	2	0	0	–	–	4	–	0	0	5	0	0	–	
Ros1	2	–	0	0	8	1	0	–	–	3	–	0	2	6	0	0	–	
Ros5	45	–	0	0	0	0	0	–	–	13	–	0	0	2	0	0	–	e
Ros6	0	–	0	0	0	0	0	–	–	4	–	0	0	0	0	0	–	
<i>Survey ponds:</i>																		
Hars 7	–	–	0	0	0	0	0	–	–	–	–	0	4	0	0	0	–	
Rem6	–	–	0	0	0	0	0	–	–	–	–	0	0	1	0	0	–	
Ros79	–	–	0	0	0	0	0	–	–	–	–	56	250	180	300	140	–	f
2004 introductions																		
<i>Intr. ponds:</i>																		
Borg3	–	0	0	0	0	0	0	–	–	–	–	3	0	0	1	0	0	–
Igel2	–	3	0	0	0	0	0	–	–	–	–	6	0	0	0	0	0	–
Igel3	–	5	0	0	0	0	0	–	–	–	–	14	0	0	0	0	0	–

Table 2.
(Continued.)

	<i>R. arvalis</i>										<i>R. temporaria</i>					Notes					
	Metamorphs		Spawn clumps								Metamorphs						Spawn clumps				
	2003	2004	2003	2004	2005	2006	2007	2008	2003	2004	2003	2004	2005	2006	2007		2008				
Sven10	-	10	0	0	0	0	0	-	-	-	1	0	0	0	0	-					
Sven15	-	1	0	0	0	0	0	-	-	-	1	0	0	0	0	-					
Survey ponds:																					
Borg1	-	-	0	0	0	0	0	-	-	-	-	0	0	0	1	-					
Borg2	-	-	0	0	0	0	0	-	-	-	-	0	2	0	0	-					
Igel8	-	-	0	0	0	0	0	-	-	-	-	2	0	0	0	-					
Igel11	-	-	0	0	0	0	0	-	-	-	-	6	0	11	1	0					
Index			1.6	1.7	2.1	1.4	1.9	3.0			0.4	0.6	0.9	0.7	1.3	1.5	g				

a, One male *R. temporaria* was heard croaking in 2004, but no spawn was seen.

b, Also 2 unidentified metamorphs.

c, 2-3 male *R. temporaria* and more than 9 *R. arvalis* were heard croaking in 2004 but no spawn was found. Three males were captured and measured: *R. arvalis* 41 and 44 mm, *R. temporaria* 49 mm (SUL).

d, Also 2 unidentified metamorphs.

e, Also 3 unidentified metamorphs.

f, So named because it was in 2003 made up by 3 ponds (Ros7, Ros8, and Ros9) that before the next breeding season were enlarged and united to create a large (1 ha) pond.

g, These are index values based on monitoring a large number of ponds in Scania, up to 70 km from the study areas. Details are given by Loman (2005, 2008).

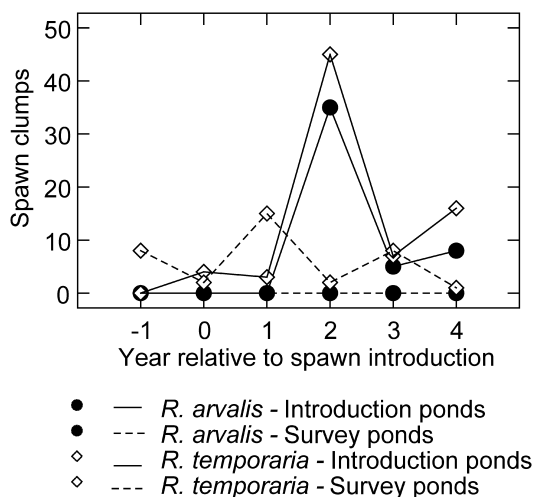


Figure 1. Summary of breeding in introduction and survey ponds (excluding pond Ros79). Year 0 is the time for experimental introduction of spawn. This took place in different years (2003 or 2004) in different areas. Thus, breeding was monitored in Year -1 for study areas Borgeby, Igelösa and Svenstorp only and it was monitored in Year 4 for Härslöv, Remmarlöv and Rosenhäll only. Spawn clumps is the total number of spawn clumps found. Counts for 2008 are not included as only two ponds were monitored in that year.

of each pond type (and actually more clumps in the survey ponds). Two years after there were *R. temporaria* spawn found in seven introduction ponds (2–12 clumps) and in two survey ponds (1 clump in each), a significant difference (Mann-Whitney *U*-test, $U = 247$, $P < 0.001$).

Discussion

It is clear that our experiment in most areas (with the exception of Svenstorp) resulted in breeding populations of one or both species in ponds where none were present earlier. This means that the terrestrial habitat was of a quality sufficient for the growth and survival of these frogs during their terrestrial phase. Even so, at most ponds the habitat was clearly not sufficient to support populations in a longer perspective. In only three cases (*R. arvalis* in Hars1, *R. temporaria* in Hars1 and Rem2) were there at least ten spawn clumps (i.e., the number of breeding females) 2 years after the introduction (table 2). In a self sustaining population, the recruits from the 20 spawn clumps we introduced should have a life time reproduction of another 20 spawn clumps. With a 50% female annual survival this corresponds to a first adult year reproduction of ten spawn clumps, suggesting that these three cases could actually meet the expectation in the short run. However, after two or three potential breeding seasons (assuming sexual maturity at an age of two years), breeding populations only remained in two of the introduction ponds (Hars1 and Rem2). In the following year, the last of the study period, only *R. temporaria* was still breeding

in one of these ponds (the one which already actually had breeding *R. temporaria* before the start of the experiment). Interestingly, these two ponds were the ponds with breeding or indications of breeding already one year after the introductions, suggesting favourable conditions for growth after metamorphosis. It thus seems we did not create a single new self sustaining population.

There were no new breeding populations established in the surrounding survey ponds. We conclude that a less than optimal terrestrial habitat in combination with isolated breeding ponds prevents (in the case of *R. arvalis*) or (in *R. temporaria*) reduces the likelihood of long term population persistence in this landscape type. On a regional scale, only *R. temporaria* is naturally found in this habitat. Although this species performed marginally better than *R. arvalis* the difference in performance was not great. A question that thus remains unanswered is whether the difference in habitat choice is because *R. temporaria* is more tolerant of the habitat or because it is a better colonizer. In the present study both species seemed to perform equally and well in the short term but poorly in the long term.

An interesting observation is that we found calling males of both species already one year after spawn was introduced in the Remmarlöv area that previously lacked frogs. They were exceptionally large for their age (table 2, note 5) but typical of first year breeders that usually are at least 2 years old. It was previously not expected that either species could reach sexual maturity at an age of 1 year (Loman, 1978; Gibbons and McCarthy, 1984; Ryser, 1988; Cherdantsev et al., 1997; Lyapkov, 2005). A possible explanation is the fact that metamorphs in this pond in the previous year were quite large (*R. a.* mean = 16.2 mm, *R. t.* mean = 16.1 mm).

These spawn introductions mimicked a single colonization event of a previously unoccupied pond. Hence we did not create a healthy, established population characterized by a normal demography with several adult age classes. The risk of extinction would probably have been less if all age classes normally found in a population were present. The fact that our populations seemed to decline over time may be partially due to this, but we cannot refrain from suggesting that a high adult mortality rate limits frogs in this landscape. Incidentally, the winter of 2005-06 was harsh and breeding populations in the entire region — not just in the studied agricultural areas — were low (population indices in table 2). Healthy populations should be, and have historically been, able to cope with such climatic events. We believe that populations lacking certain cohorts (such as our introduced populations) are more vulnerable to malign climatic influences. However, to successfully colonize an area or to re-colonize after a catastrophic extinction a population must be able to cope with this situation. As a colonization mimic our experiment represented what must be considered an unusually favourable event — the simultaneous colonization of 20 pairs per pond!

The combined conclusion from this and our previous study (Loman and Lardner, 2006) is that features of the terrestrial habitat, rather than the aquatic, explain the poor success of these species in the agricultural landscape we studied. This does not mean that increasing the number of high quality ponds would be a wasted effort

when trying to make the landscape more suitable for frogs. We believe that part of the problem lies in the metapopulation structure, or at least pond isolation. If so, a denser network of suitable ponds would indeed contribute to increased possibilities of re-colonization should a local population go extinct. This strategy has been successfully adopted for amphibian conservation efforts (Petranka et al., 2007).

Still, we think that our study foremost emphasizes the importance of suitable terrestrial habitats for these species. Our study ponds were surrounded by a 1-10 m margin of non-field habitat, usually unmanaged grassland and some bushes. Apart from that, most habitat within the next few hundred meters was cropped fields. One exception was Rem2 (the second most successful introduction) where about 1 ha of grassland was adjacent to the pond. Within 1 km of most ponds there was some alternative habitat, mainly gardens in the vicinity of farm houses. This was not enough to support these populations.

While some studies have failed to find a negative influence of agriculture on amphibian diversity (Gagne and Fahrig, 2007), most have found agricultural habitats to be generally poor for frogs (Van Buskirk, 2005; Werner et al., 2007a; Piha et al., 2007). Diverse results are however not unexpected in cases like this where different agricultural landscapes are studied and also compared to different null habitats. Few studies (and this is not one of them) have confirmed a true metapopulation structure for amphibians in a study landscape (Smith and Green, 2005). However, the pond isolation we suggest was a problem for the populations we founded has also been identified by several other studies as a factor negatively affecting amphibian presence (Ficetola and De Bernardi, 2004; Cushman, 2006; Becker et al., 2007). Indeed, local extinction and re-colonization has commonly been shown for amphibian communities (Werner et al., 2007b). Of particular interest is the study by Piha et al. (2007) where the adverse effect of agricultural landscapes was evident only in areas with a long history of agriculture. This suggests that the combination of an agricultural habitat and isolated breeding ponds is particularly detrimental to the long-term persistence of amphibian populations.

Acknowledgements

The study was financed by The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning. Thanks to Shane Siers who helped improve the language.

References

- Becker, C., Fonseca, C., Haddad, C., Batista, R., Prado, P. (2007): Habitat split and the global decline of amphibians. *Science* **318**: 1775-1777.
- Bennett, A., Radford, J., Haslem, A. (2006): Properties of land mosaics: implications for nature conservation in agricultural environments. *Biol. Conserv.* **133**: 250-264.
- Berglund, B. (1976): Skånes sällsynta groddjur. *SNV PM* **765**: 1-114.
- Bonin, J., DesGranges, J.-L., Rodrigue, J., Quillet, M. (1997): Anuran species richness in agricultural landscapes of Quebec: foreseeing long-term results of road-call surveys. In: *Amphibians in Decline. Canadian Studies of a Global Problem*, p. 141-149. Green, M., Ed., St., Louis, Miss., Soc. Study Amph. Rept.

- Cherdantsev, V.G., Lyapkov, S.M., Cherdantseva, E.M. (1997): Mechanisms accounting for the pattern of fecundity formation in the frog, *Rana arvalis* Nilss. *Russ. J. Zool.* **1**: 30-40.
- Cushman, S. (2006): Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biol. Conserv.* **128**: 231-240.
- Denoel, M., Lehmann, A. (2006): Multi-scale effect of landscape processes and habitat quality on newt abundance: implications for conservation. *Biol. Conserv.* **130**: 495-504.
- Ficetola, G., De Bernardi, F. (2004): Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biol. Conserv.* **119**: 219-230.
- Gagne, S., Fahrig, L. (2007): Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada. *Landsc. Ecol.* **22**: 205-215.
- Gibbons, M.M., McCarthy, T.K. (1984): Growth, maturation and survival of frogs *Rana temporaria* L. *Holarc. Ecol.* **7**: 419-427.
- Gray, M.J., Smith, L.M. (2005): Influence of land use on postmetamorphic body size of Playa lake amphibians. *J. Wildl. Manag.* **69**: 515-524.
- Lehtinen, R.M., Galatowitsch, Tester, J.R. (1999): Consequences of habitat loss and fragmentation for wetland amphibian assemblages. *Wetlands* **19**: 1-12.
- Loman, J. (1978): Growth of brown frogs *Rana arvalis* and *Rana temporaria* in south Sweden. *Ekol. Polska* **269**: 287-296.
- Loman, J. (1979): Food feeding rates and prey size selection in juvenile and adult frogs *Rana arvalis* and *Rana temporaria*. *Ekol. Polska* **27**: 581-602.
- Loman, J. (2005): Inventering av åkergroda och vanlig groda i Skåne 1989-2003. Trender och utvärdering av metoder. Länsstyrelsen i Skåne län, Malmö, Sweden.
- Loman, J. (2008): Studies on the moor frog (*Rana arvalis*) in south Sweden. *J. Fld. Herp. Suppl.* **19**: 195-206.
- Loman, J., Lardner, B. (2006): Does pond quality limit frogs *Rana arvalis* and *R. temporaria* in agricultural landscapes? A field experiment. *J. App. Ecol.* **43**: 690-700.
- Lyapkov, S.M. (2005): Geographical and local variation of reproductive and demographic characteristics in brown frogs. *Herpetologica Petropolitana, Proceedings of the 12th Ordinary General Meeting of the Societas Europaea Herpetologica, August 12-16, 2003, St. Petersburg, Russia* 187-190.
- Petranka, J., Harp, E., Holbrook, C., Hamel, J. (2007): Long-term persistence of amphibian populations in a restored wetland complex. *Biol. Conserv.* **138**: 371-380.
- Piha, H., Luoto, M., Merila, J. (2007): Amphibian occurrence is influenced by current and historic landscape characteristics. *Ecol. Appl.* **17**: 2298-2309.
- Ryser, J. (1988): Determination of growth and maturation in the common frog, *Rana temporaria*, by skeletochronology. *J. Zool.* **216**: 673-685.
- Smith, M., Green, D. (2005): Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* **28**: 110-128.
- Van Buskirk, J. (2005): Local and landscape influence on amphibian occurrence and abundance. *Ecology* **86**: 1936-1947.
- Werner, E., Skelly, D., Relyea, R., Yurewicz, K. (2007a): Amphibian species richness across environmental gradients. *Oikos* **116**: 1697-1712.
- Werner, E., Yurewicz, K., Skelly, D., Relyea, R. (2007b): Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* **116**: 1713-1725.