

Microevolution and maternal effects on tadpole *Rana temporaria* growth and development rate

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Abstract

Can variation in egg size explain the local variation in tadpole growth and development of the common frog *Rana temporaria* or are other mechanisms, e.g. microevolution, involved? To study this, tadpoles were raised in outdoor tanks. Each tank housed tadpoles from one clutch. Eggs were collected during 2 years from six different ponds and their sizes were measured. Large eggs gave rise to tadpoles that grew and developed faster than those hatched from small eggs. Tadpoles from large eggs thus metamorphosed earlier but, because they grew for a shorter time, size at metamorphosis was not affected by initial egg size. Tadpoles from different ponds differed in strategy; after correcting for egg size effects, tadpoles from some ponds tended to metamorphose earlier and at a larger size than those from others. These ponds occasionally dry out during or before the tadpoles' period of metamorphosis. I argue that the detected pond differences are genetically based and represent a case of microevolution.

Key words: egg size, metamorphosis, drying ponds, amphibians, frogs, *Rana temporaria*

INTRODUCTION

Many females have the option to balance their reproductive investment between quantity (many young) and quality (large young) (Roff, 1992). The benefit of a large clutch is obvious while the advantage of large offspring is not always so, and actually there are instances where normalizing selection on average size seems to occur (Congdon *et al.*, 1999). The present study attempted to investigate the effects, and possible benefits, of egg size for the individual offspring.

Egg size is not necessarily genetically determined. Large eggs may be the offspring of a large and old (Gibbons & MacCarthy, 1986; Joly, 1991) or well-fed female (Girish & Saidapur, 2000). Non-genetic effects of the mother on the individual young have been termed maternal effects (Bernardo, 1996; Falconer & Mackay, 1996; Rossiter, 1996). In studies of amphibians this usually refers to egg size (Parichy & Kaplan, 1992; Kaplan, 1998). Correcting for egg size (which may be non-genetic) increases precision when studying the genetic component of characters (like tadpole growth and development) that may also be influenced by egg size. This makes it feasible to analyse the possible microevolution of these characters.

Previous studies made in southern Sweden have demonstrated differences in development and growth rate between common frog *Rana temporaria* L. tadpoles from different ponds (Loman, in press). In addition,

these differences persisted when tadpoles were raised under standardized conditions in tanks (pers. obs.). Thus, the differences must have been present in the eggs laid in the different source ponds. These differences could be either of genetic or phenotypic origin. An obvious example of the latter possibility would be if eggs laid in some ponds are larger, and therefore develop faster (Berven & Chadra, 1988). Thus, such a hypothetical egg size difference between ponds, may not be genotypic but it could also result from differences in growth rate or age structure between females from different ponds in this area. This has been shown for neighbouring populations of common frogs by Joly (1991). Reading (1988) suggested that size differences between common toads *Bufo bufo* L. from two populations were the result of differences in growing conditions.

The second purpose of this study was to distinguish genetic and non-genetic explanations for population differences in growth and development rate of the common frog tadpole. The populations studied are from the same area where population differences in the field and in tanks were observed (Loman, in press). Egg size effects were measured and this information used to investigate possible residual pond effects, i.e. pond effects when pond differences in egg size are corrected for. Therefore, clutches with large and small eggs were selected from study ponds and raised in a 'common garden' experiment (Fauth, 1998).

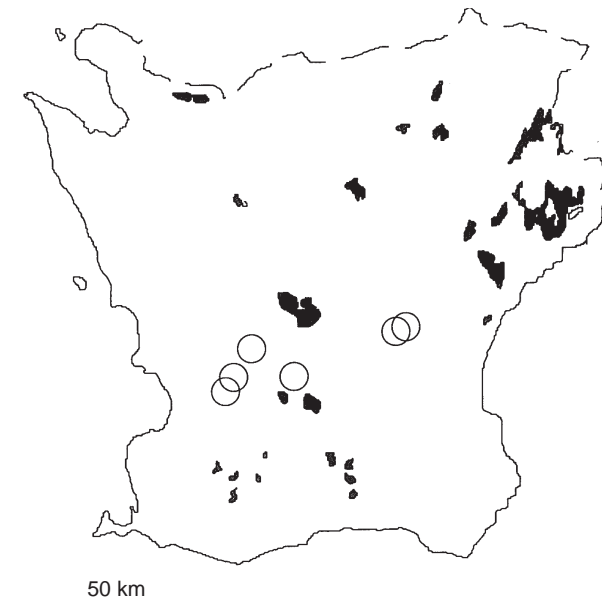


Fig. 1. Map of Skåne in south Sweden showing the six source ponds.

METHODS

Eggs of the common frog were collected from ponds in the southernmost part of Sweden, Skåne. All ponds were sampled in 1993 and 1994. The eggs used came from 6 different ponds. The most south-western pond was close to Lund while the most north-eastern pond was close to Svensköp in central Skåne, 40 km away (Fig. 1). The growth and development rate of tadpoles was determined by raising them in 80 l outdoor tanks at the field station (which is situated in the same area as the source ponds).

Eggs from 4 spawn clumps were used from each pond. Two clumps with large eggs (compared to those in other clumps in each pond) and 2 with small eggs were selected. Hence, with 6 ponds, 4 clutches per year and 2 years, there was a total of 48 experimental units (tanks). In the actual analyses the measured egg size (not size category; small *vs* large) was used as input. From each spawn clump, 20 newly hatched tadpoles were picked at random and raised in an 80 l tank. Because eggs may increase in size (King & Kaplan, 1997), only eggs from spawn up to 4 days old were used. Optical distortions in the jelly tend to increase random error when measuring egg size. To minimize this, the eggs were separated in a single layer and immersed in water to a depth equal to egg diameter (including jelly) when measured with callipers. There was only little within-clump variation in egg size (clutch identity accounted for 78% of egg size variation, r^2 in a 1-way ANOVA). Therefore, the average egg size in a sample of 15 eggs was computed for each clump and used as a measure for the size of the eggs in 1 clutch.

Eggs in different ponds were laid at different dates in

the field. To compensate for this, early laid eggs were kept in a refrigerator (at *c.* 4°C) for up to 7 days. Hatching was thus synchronized and date for metamorphosis could be used as a measure of development rate. Hatching took place on 26 April 1993 and 20 April 1994.

All tadpoles were measured on 25 May 1993 and 6 June 1994, respectively. For each tadpole, body length and hind leg length were measured. Hind leg length was used to compute 'relative leg length': hind leg length divided by body length. This was used as a measure of development rate.

When the tadpoles approached metamorphosis, the tanks were checked daily. Tadpoles close to metamorphosis, as indicated by a tail shorter than body length, were removed, measured and released. Measurements were taken of weight, body length and tail length. If the tail was >30% of body length, the next day was scored as the day of metamorphosis. Individual measurements on length and weight were combined to a general size index by principal component analysis; the scores of first PCA-axis was used as this index.

The independent effects of year, egg size, and pond was tested with a 3-way ANCOVA. Average tank values of tadpole and metamorph performance was used as input. All considered variables of tadpole and metamorph performance were significantly affected by year. This was expected as 1993 was a warmer year than 1994, and year effects were not within the scope of this study, these effects are not discussed and tested further. However, the year effect is included in the ANCOVA models as it is necessary to compensate for this when analysing the other factors.

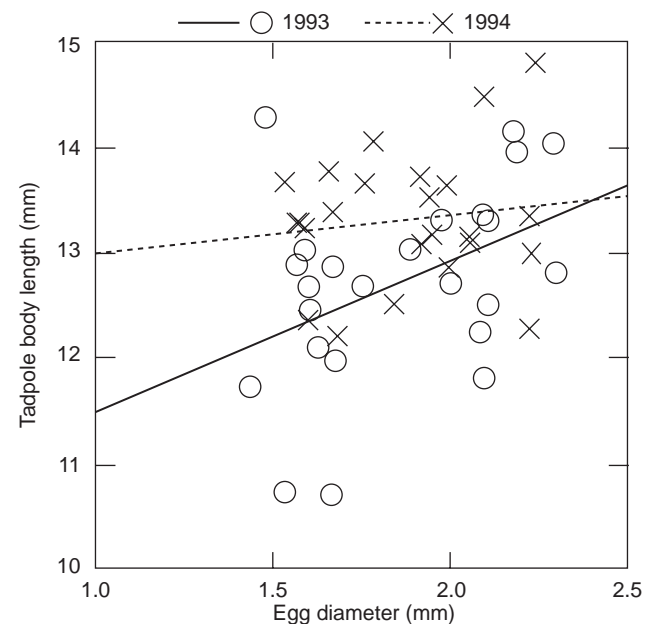


Fig. 2. Effect of *Rana temporaria* egg size on tadpole size (body length on 25 May 1993 and 6 June 1994) when controlling for year. Each symbol is the average value for individuals in one tank. the linear regression is fitted independently for both years.

Table 1. Independent effects of egg size, pond, and year on *Rana temporaria* tadpole and metamorph performance, tested with a three-way ANCOVA (two factors and one covariate). For all response variables except tadpole body length, all interactions were not significant and removed. For tadpole body length, the interaction Year*pond was significant, d.f. = 5:35, $F=3.35$, $P=0.014$ and the effects of egg size and pond therefore analysed separately for the 2 years. In these tests the Pond*egg size interactions were not significant and removed

		Egg size			Pond			Year		
		d.f.	F	P	d.f.	F	P	d.f.	F	P
Tadpole body length	1993	1:17	10.01	0.006	5:17	4.48	0.009			
	1994	1:17	1.32	0.27	5:17	1.01	0.44			
Relative tadpole hind leg		1:40	16.2	<0.001	5:40	1.43	0.24	1:40	5.00	0.031
Time for metamorphosis		1:40	15.2	<0.001	5:40	3.31	0.014	1:40	513	<0.001
Metamorph size		1:40	0.003	0.96	5:40	1.62	0.18	1:40	22.6	<0.001

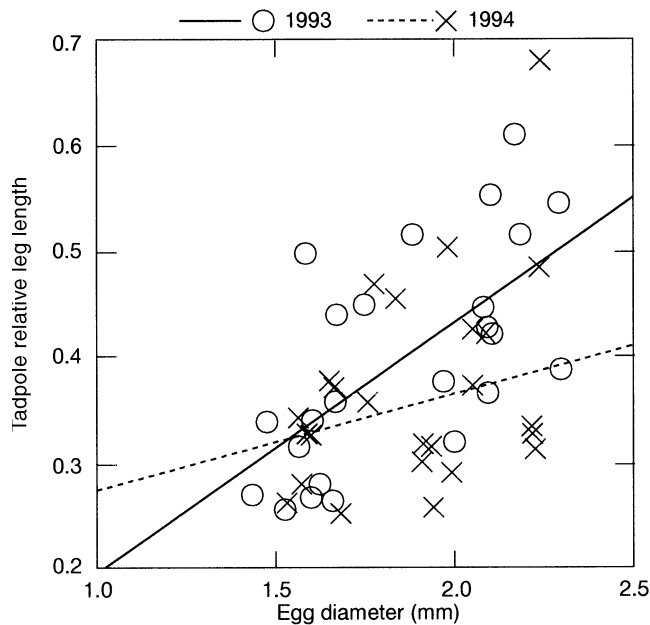


Fig. 3. Effect of *Rana temporaria* egg size on relative leg length (hind leg length divided by tadpole body length measured on 25 May 1993 and 6 June 1994).

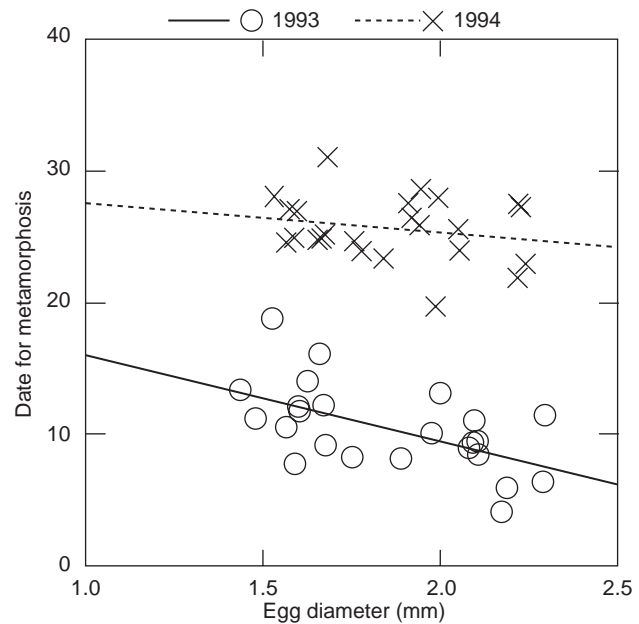


Fig. 4. Effect of *Rana temporaria* egg size on date for metamorphosis. y -values, days from 1 June.

RESULTS

Effects of egg size

When measured at an age of *c.* 1 month, tadpoles hatching from large eggs were larger than those hatching from small eggs (Table 1, Fig. 2). Tadpoles from large eggs also developed faster (a larger relative leg length) (Table 1, Fig. 3) and metamorphosed earlier than those hatched from small eggs (Table 1, Fig. 4). However, there was no influence of egg size on metamorph size (Table 1, Fig. 5).

Effects of pond

The interaction between year and pond affected tadpole size significantly (Table 1). This was expressed as a significant effect of pond on tadpole size in 1993 (but not in 1994), when controlling for egg size (Table 1).

There was no pond effect on early tadpole development (relative leg length) but later, time for metamorphosis did differ significantly between ponds (Table 1). There was no significant effect of pond on size at metamorphosis (Table 1).

Correlations between different traits

For all tanks, the four measures of performance were recomputed, correcting for egg size and year effects. This was done using residual from the ANCOVA model with main effects only of year and egg size. After that, the residuals were averaged pond wise, yielding pond specific measures of tadpole growth and development rate. The measures of relative leg length and time for metamorphosis were (negatively) correlated (Table 2); they both represent aspects of development rate. However, these two measures were also correlated with tadpole size (growth rate), fast-growing tadpoles developing quicker and metamorphosing earlier (Table 2,

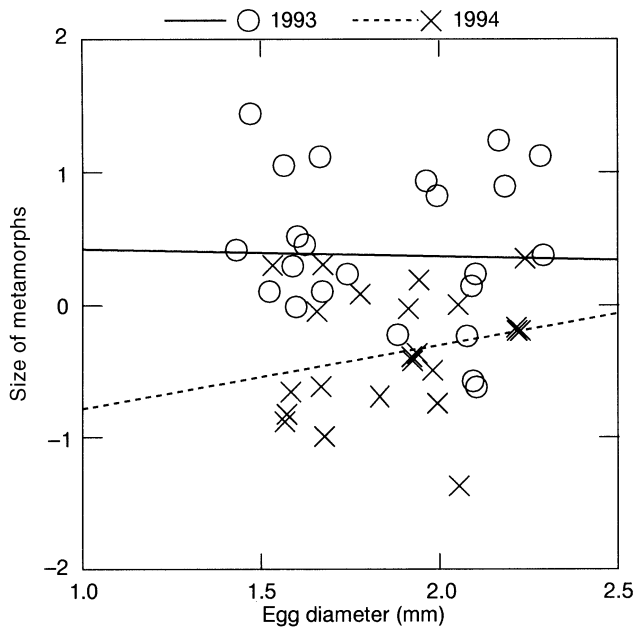


Fig. 5. Effect of *Rana temporaria* egg size on size at metamorphosis. Size is computed as the principal component of body length and weight.

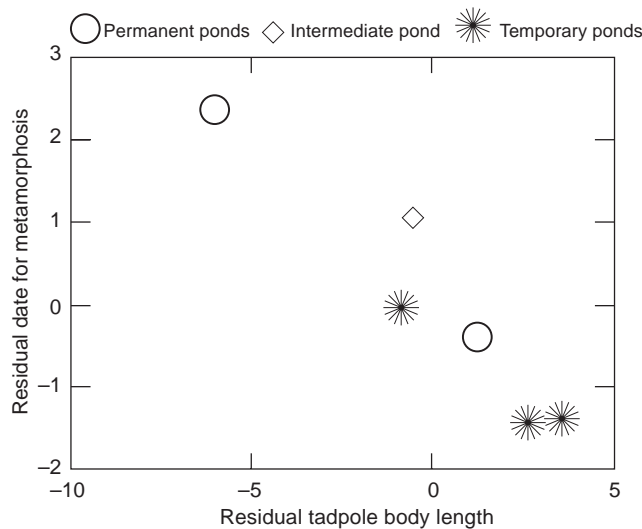


Fig. 6. Relation between day of metamorphosis and *Rana temporaria* tadpole body size (both corrected for egg size and year). Each symbol is the average tank value for one pond. The permanent ponds never dried (during 8 years of monitoring). The intermediate pond dried before or during metamorphosis in 2 out of 8 years. The three temporary ponds dried out in 6 out of 6, 5 out of 6 and in 5 out of 7 years respectively.

Fig. 6). The correlations with size at metamorphosis were less consistent.

In the field, variation in time for metamorphosis is, in addition to the variation that is discussed here (i.e. corrected for the egg size effect), also due to among-pond variation in egg size. Such variation does exist for

Table 2. Correlations between residual measures of *Rana temporaria* tadpole performance. The residuals represent the actual values, corrected for year and egg size effects. There are six observations (ponds) for all tests. All correlations are significant ($P < 0.001$) except those marked *, both $P > 0.20$. Bartlett's test for multiple comparisons, $\chi = 24.99$, $P < 0.001$

	Tadpole size	Relative leg size	Date for metamorphosis
Relative leg size	0.98		
Date for metamorphosis	-0.95	-0.96	
Metamorph size	0.54*	0.38*	-0.47*

R. temporaria in the study area (Loman, 2001). For the six ponds, in this study, there was no correlation between these two sources of variation; average pond egg size (from Loman, 2001) and residual day of metamorphosis, as measured in the present study ($r = -0.26$, $n = 6$, $P = 0.63$).

DISCUSSION

Egg size effects

This study clearly shows that egg size does affect tadpole growth and development. Tadpoles hatched from large eggs grew and developed faster, metamorphosing before those hatched from smaller eggs. However, because of the longer development of tadpoles from small eggs, size at metamorphosis was similar for all tadpoles, regardless of egg size (Fig. 7). The effect of egg size on development rate may represent a genetic variation in development rate to the extent the variation in egg size is genetic. It may also represent a non-genetic maternal effect; egg size may possibly depend on female condition and/or age. This study does not allow a separation of these effects.

This pattern of egg size effects is similar to those that have been found for differences in environmental quality (e.g. food resources) (Blouin, 1992; Beck, 1997; Merilä, Laurila, Laugen *et al.* 2000; pers obs.). Altogether, metamorphs originating from large eggs seem to have a head start. Goater & Vandebos (1997) have shown for wood frog *Rana sylvatica* that this size advantage remains at least to the end of the first growing season.

Some other studies have yielded similar results. In a study by Parichy & Kaplan (1992), initially small tadpoles (*Bombina orientalis*) presumably hatched from small eggs (Williamson & Bull, 1989; Gollmann & Gollmann, 1994; Parichy & Kaplan, 1995), grew and developed similarly to large larvae when raised under good food conditions. However, when raised under poorer food conditions they metamorphosed later and at a smaller size. Thus, egg size, as in my study, affected both growth and development rate. However, in the end those tadpoles, in contrast to those in my study, under resource stress 'made' a compromise between time and

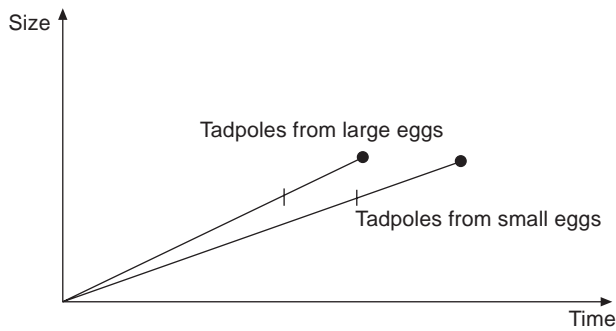


Fig. 7. Growth pattern for *Rana temporaria* tadpoles hatched from large and small eggs. Closed circle, metamorphosis; vertical bar, an (arbitrary) development stage (it symbolizes that at some point of time fast developing tadpoles (upper line) have passed this stage but more slowly developing have not yet done so).

size sacrifice and slowly developing tadpoles metamorphosed at a smaller size than those developing faster. A study by Semlitsch & Smiedhausen (1994) showed the opposite interaction between resource level and the effect of egg (actually hatchling) size on *Rana lessonae* tadpole growth rate, age and size at metamorphosis; at high food levels the larger hatchlings performed better, but at low food levels no size effect was observed.

Berven & Chadra (1988) showed that in the wood frog, tadpoles from small eggs always metamorphosed later than those hatching from large eggs. However, with abundant resources they did not metamorphose until they were even larger than those hatching from large eggs! With poor resources, they acted like the *Bombina* larvae of Parichy & Kaplan (1992) and metamorphosed at a smaller size than those hatching from large eggs. The larvae in the present study thus behaved like those of Berven & Chadra (1988), assuming that they were raised under intermediate resource levels.

Not all studies have detected effects of egg size on tadpole growth and development. Negative or non-significant results have been reported by Crump (1984) (*Hyla crucifer*), Surova & Cherdantsev (1987) (*Rana temporaria*), Tejedo & Reques (1992) (*Bufo calamita*) and Semlitsch & Smiedhausen (1994) (*Rana esculenta*).

Merilä, Laurila, Phakala *et al.* (2000) have shown that the amount of food during the first 4 days of *Rana temporaria* tadpole life influences age (and size) at metamorphosis. The effect found may thus be a direct effect of the nutrients and energy that come with a large egg.

Egg size may affect other aspects of tadpole fitness. *Bombina orientalis* tadpoles hatched from large eggs and raised in cold water were less susceptible to predation than those hatched from small eggs. However, the opposite was true when tadpoles were raised in warmer water (Kaplan, 1992). Tadpoles hatched from large eggs of several Greek species were better at surviving starvation than those hatched from small eggs (Sofianidou, Pirovetsi-Vassiliadous & Kiriakopoulou-Sklavouna,

1997). On the other hand, at low pH, large eggs had a lower hatchability than small ones in wood frogs (Pierce, Margolis & Nirtaut, 1987). More examples are cited in a review by Kaplan (1998). Thus egg size effects often interact with environmental quality, making it difficult to separate 'negative' results from demonstrated effects unless a very detailed analysis of the influence environmental variation is made. My study yielded a clear effect of egg size, but the design does not allow an analysis of any interactions with growing conditions.

Given that large eggs results in fast growth and development and early metamorphosis, what is the importance of this for fitness? A fast growth may reduce the time the tadpole is vulnerable to size-limited predators (Lardner & Loman, 1995; Werner & Anholt, 1996). Fast development and early metamorphosis reduces the risk of drying from desiccation, should the pond dry early (Cooke, 1985; Loman, 1996). There are also studies suggesting early metamorphosing individuals are larger at first reproduction than late metamorphosing ones (*Ambystoma talpoideum*; Semlitsch, Scott & Pechman, 1988). All these effects are probably advantageous.

Pond effects

Tadpoles from different ponds performed differently, in addition to effects from any egg size differences between ponds. This effect was only significant for time for metamorphosis and, in 1993, for tadpole body size. Interestingly, comparing different ponds, these effects had not the character of a trade-off. Rather, even after correcting for egg size differences, tadpoles in some ponds grew fast and metamorphosed early (Fig. 6). Either tadpoles from these ponds had a higher overall quality (provided these traits are advantageous) or tadpoles in these ponds balance these traits with some behavioural trait. A possible scenario follows. For some frog species it has been shown or suggested that tadpoles reduce activity in the presence of predators (Skelly & Werner, 1990; Semlitsch & Reyer, 1992; Anholt & Werner, 1999), thus reducing growth rate (Skelly, 1992; Laurila & Kujasalo, 1999). It is possible that low activity level is a fixed trait for tadpoles from some ponds (and thus persisted when raised in tanks). Such a situation has been demonstrated for the moor frog *Rana arvalis* (Lardner, 1998). One could expect such a trait to be present in ponds where predators are often encountered. So, ponds with slowly growing and slowly developing tadpoles could be ponds where the tadpoles have a trait for carefulness (and feed slowly). Therefore these tadpoles grow and develop slowly.

There is also some evidence for a more specific scenario. In this study, ponds with fast growing and fast developing tadpoles (after correcting for egg size effects) were those that regularly dry out in dry summers (Fig. 6). It makes sense that tadpoles in temporary ponds develop quickly, but why also grow larger? The fate of the pond is conditional and the response (a faster

development) is at least partly facultative (Laurila & Kujasalo, 1999; Loman, 1999; Merilä, Laurila, Pakkala, *et al.* 2000). Also, some studies suggest that increased development rate has a price, namely decreased growth rate (Laurila & Kujasalo 1999; Merilä, Laurila, Pakkala *et al.* 2000). Thus, high growth rate gives tadpoles in potentially temporary ponds the possibility of sacrificing some of their potential size for an early metamorphosis if necessary. This was not necessary in the experiment as the water level remained high throughout the metamorphosis period.

Was this residual (after correcting for egg size and year) pond effect genetic, representing a case of microevolution between ponds? Genetic differentiation between salamander larvae (Semlitsch & Wilbur, 1989; Semlitsch, Harris & Wilbur, 1990) and frog tadpoles (Reh & Seitz, 1989; Regnaut, 1997) from nearby ponds has indeed been demonstrated. Also, Travis, Emerson & Blouin (1987) have shown that variation in larval growth and development rate can indeed be the result of genetic variation. In a previous study (*pers. obs.*), source pond affected tadpole size, relative leg length and date of metamorphosis significantly. The previous results included the effect of possible source pond differences in egg size and other maternal effects. Altogether, pond effects could be (non-exclusive alternatives) genetic, mediated by egg size (genetic and non-genetic) and, hypothetically, mediated by pond specific substances (taken up by the females and passed on to the eggs) that affect tadpole performance (the latter alternative is thought unlikely). The present study shows that pond effects remain, even after correction for egg size effects. I have previously argued that these pond effects were most probably of genetic origin. The present findings, where effects of egg size are corrected for, make the case stronger. More support comes from the fact that the pattern of variation may, as suggested above, be explained in terms of local adaptations.

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REFERENCES

- Anholt, B. R. & Werner, E. E. (1999) Density-dependent consequences of induced behavior. In *The ecology and evolution of inducible defences*: 218–230. Tollrian, R. & Harwell, C. D. (Eds). Princeton, NJ: Princeton University Press.
- Beck, C. W. (1997). Effects of changes in resource level on age and size at metamorphosis in *Hyla squirella*. *Oecologia (Berl.)* **112**: 187–192.
- Bernardo, J. (1996). Maternal effects in animal ecology. *Am. Zool.* **36**: 83–105.
- Berven, K. A. & Chadra, B. G. (1988). The relationship among egg size density and food level on larval development in the wood frog *Rana sylvatica*. *Oecologia (Berl.)* **75**: 67–72.
- Blouin, M. S. (1992). Comparing bivariate reaction norms among species: time and size at metamorphosis in three species of *Hyla* (Anura: Hylidae). *Oecologia (Berl.)* **90**: 288–293.
- Congdon, J. D., Nagle, R. D., Dunham, A. E., Beck, C. W.-K. O. M. & Yeomans, S. R. (1999). The relationship of body size to survivorship of hatchling snapping turtles (*Chelydra serpentina*) an evaluation of the 'bigger is better' hypothesis. *Oecologia (Berl.)* **121**: 224–235.
- Cooke, A. S. (1985). The deposition and fate of spawn clumps of the common frog *Rana temporaria* at a site in Cambridgeshire 1971–1983. *Biol. Conserv.* **32**: 165–187.
- Crump, M. (1984). Intra clutch egg size variability in *Hyla crucifer* Anura Hylidae. *Copeia* **1984**: 302–308.
- Falconer, D. S. & Mackay T. F. C. (1996). *Quantitative genetics*. Harlow: Longman.
- Fauth, J. (1998). Investigating geographical variation in interspecific interactions using common garden experiments. *Experimental ecology. Issues and perspectives*: 394–415. Resetarits, W. J. Jr & Bernardo, J. (Eds). Oxford: Oxford University Press.
- Gibbons, M. M. & McCarthy T. K. (1986). The reproductive output of frogs *Rana temporaria* (L.) with particular reference to body size and age. *J. Zool. (Lond.)* **209**: 579–593.
- Girish, S. & Saidapur, S. K. (2000). Interrelationship between food availability, fat body, and ovarian cycles in the frog, *Rana tigrina*, with a discussion of the role of fat body in anuran reproduction. *J. exp. Zool.* **286**: 487–493.
- Goater, C. P. & Vandebos, R. E. (1997). Effects of larval history and lungworm infection on the growth and survival of juvenile wood frogs (*Rana sylvatica*). *Herpetologica* **53**: 331–338.
- Gollmann, G. & Gollmann, B. (1994). Offspring size variation in a hybrid zone of Australian frogs (*Geocrinia laevis* complex, Myobatrachinae). *Amphib.-Reptilia* **15**: 343–350.
- Joly, P. (1991). Variation in size and fecundity between neighbouring populations in the common frog *Rana temporaria*. *Alytes* **9**: 79–88.
- Kaplan, R. (1992). Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. *Oikos* **73**: 280–288.
- Kaplan, R. H. (1998). Maternal effects, developmental plasticity, and life history evolution. *Maternal effects as adaptations*: 244–260. Mousseau, T. A. & Fox, C. W. (Eds). Oxford: Oxford University Press.
- King, E. G. & Kaplan, R. H. (1997). Estimating ovum size in amphibians: egg size increases differently among species during early development. *J. Herpetol.* **31**: 299–302.
- Lardner, B. (1998). Plasticity or fixed adaptive traits? Strategies for predation avoidance in *Rana arvalis* tadpoles. *Oecologia (Berl.)* **117**: 119–126.
- Lardner, B. & Loman, J. (1995). Predation on *Rana* and *Bufo* tadpoles: predator species and tadpole size effects. *Mem. Soc. fauna Flora Fenn.* **71**: 149.
- Laurila, A. & Kujasalo, J. (1999). Habitat duration, predation risk and phenotypic plasticity in common frog (*Rana temporaria*) tadpoles. *J. Anim. Ecol.* **68**: 1123–1132.
- Loman, J. (1996). Övervakningsprogram för brungrödor i Skåne. *Rapp. Miljöövervakningen Malmöhus län* **7**: 1–47.
- Loman, J. (1999). Early metamorphosis in common frog *Rana temporaria* tadpoles at risk of drying: an experimental demonstration. *Amphib.-Reptilia* **20**: 421–430.
- Loman, J. (2001). Local variation in *Rana temporaria* egg and clutch size – adaptations to pond drying? *Alytes* **19**: 45–52.
- Loman, J. (In press). Temperature, genetic and hydroperiod effect on metamorphosis of brown frogs *Rana arvalis* and *R. temporaria* in the field. *J. Zool. (Lond.)*.
- Merilä, J., Laurila, A., Laugen, A. T., Räsänen, K. & Pakkala, M. (2000). Plasticity in age and size at metamorphosis in *Rana*

- temporaria* – comparison of high and low latitude populations. *Ecography* **23**: 457–465.
- Merilä, J., Laurila, A., Pakkala, M., Räsänen, K. & Laugen, A. T. (2000). Adaptive phenotypic plasticity in timing of metamorphosis in the common frog *Rana temporaria*. *Ecoscience* **7**: 18–24.
- Parichy, D. M. & Kaplan, R. H. (1992). Maternal effects on offspring growth and development depend on environmental quality in the frog *Bombina orientalis*. *Oecologia (Berl.)* **91**: 579–586.
- Parichy, D. M. & Kaplan, R. H. (1995). Maternal investment and developmental plasticity: functional consequences for locomotor performance of hatchling frog larvae. *Funct. Ecol.* **4**: 606–617.
- Pierce, B. A., Margolis, M. A. & Nirtaut, L. J. (1987). The relationship between egg size and acid tolerance in *Rana sylvatica*. *J. Herpetol.* **21**: 178–184.
- Reading, C. J. (1988). Growth and age at sexual maturity in common toads (*Bufo bufo*) from two sites in Southern England. *Amphib.-Reptilia* **9**: 277–288.
- Regnaut, S. (1997). *Population structure of the moor frog (Rana arvalis) in a Baltic sea archipelago*. Lund University, Lund.
- Reh, W. & Seitz, A. (1989). Untersuchungen zum Einfluss der Landesnutzung auf die genetische Struktur von populationen des Grasfrosches (*Rana temporaria* L.). In Kuttler, W. (Ed.). *Verhandlung Gesellschaft für Ökologie XVIII, Essen 1988*: 793–797. Göttingen: Gesellschaft für Ökologie.
- Roff, D. A. (1992). *The evolution of life histories. Theory and analysis*. New York: Chapman & Hall.
- Rossiter, M. (1996) Incidence and consequences of inherited environmental effects. *Annu. Rev. Ecol. Syst.* **27**: 451–476.
- Semlitsch, R. D., Harris, R. N. & Wilbur, H. M. (1990). Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. *Evolution* **44**: 1604–1613.
- Semlitsch, R. D. & Reyer, H.-U. (1992). Performance of tadpoles from the hybridogenetic *Rana esculenta* complex: interactions with pond drying and interspecific competition. *Evolution* **46**: 665–676.
- Semlitsch, R. D. & Schmiedhausen, S. (1994). Parental contributions to variation in hatchling size and its relationship to growth and metamorphosis in tadpoles of *Rana lessonae* and *Rana esculenta*. *Copeia* **1994**: 406–412.
- Semlitsch, R., Scott, D. E. & Pechmann, J. H. K. (1988). Time and size at metamorphosis related to fitness in *Ambystoma talpoideum*. *Ecology* **69**: 184–192.
- Semlitsch, R. D. & Wilbur, H. M. (1989). Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution*, **43**: 105–112.
- Skelly, D. & Werner, E. E. (1990). Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* **71**: 2313–2322.
- Skelly, D. K. (1992). Field evidence for a cost of behavioral antipredator response in a larval amphibian. *Ecology* **73**: 704–708.
- Sofianidou, T. S., Pirovetsi-Vassiliadou, M. & Kiriakopoulou-Sklavounou, P. (1977). Starvation experiments on tadpoles and some newly metamorphosed species of Anura, *Bombina variegata*, *Bufo viridis*, *Hyla arborea*, *Rana dalmatina*. *Acta. Ann. Fac. Phys. Math. Aristotelian Univ. Thessaloniki.* **17**: 141–152.
- Surova, G. S. & Cherdantsev, V. G. (1987). Embryonic morphs in the populations of brown frogs egg size and rates of larval growth in Moscow district USSR *Rana temporaria* and *Rana arvalis*. *Zool. Zh.* **66**: 1864–1872.
- Tejedo, M. & Reques, R. (1992). Effects of egg and density on metamorphic traits in tadpoles of the natterjack toad (*Bufo calamita*). *J. Herpetol.* **26**: 146–152.
- Travis, J., Emerson, S. B. & Blouin, M. (1987). A quantitative analysis of larval life-history traits in *Hyla crucifer*. *Evolution* **41**: 145–156.
- Werner, E. E. & Anholt, B. R. (1996). Predator-induced behavioural indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* **1**: 157–169.
- Williamson, I. & Bull, C. M. (1989). Life history variation in a population of the Australian frog *Ranidella signifera*: egg size and early development. *Copeia* **1989**: 349–356.