

Primary and secondary phenology. Does it pay a frog to spawn early?

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Abstract

This study examines the consequences of variation in the laying and hatching date for the time of metamorphosis in the common frog *Rana temporaria*. Field data are presented showing that eggs laid early tend to take longer to develop. Thus, the time advantage for early eggs is reduced at the time of hatching. There was an among-year variation in this phenomenon; it was not manifest in a phenologically late year. Also, field data revealed that mortality due to pond freezing is a real risk for early laid eggs. Finally, two experiments in tanks analyse the effects of hatching date variation for the time of metamorphosis. (1) When hatching was experimentally delayed by 7 or 11 days, this resulted in later metamorphosis, however, by only 2 and 5 days, respectively. (2a) When tadpoles from the same pond that naturally hatched at different times were compared, it was found that a hatching time difference of 6 days resulted in later metamorphosis by 2 days only. (2b) A comparison of tadpoles from two different ponds that hatched 11 days apart also resulted in only 2 days' difference in metamorphosis. In this case, the later but faster developing tadpoles metamorphosed at a smaller size. I suggest that eggs from these two ponds differed genetically in the growth and development strategy. Despite the obvious risks, and the moderate gain in terms of early metamorphosis, frogs breed dangerously early in spring. Possible reasons for this are discussed. These include external selective forces that promote early metamorphosis (also at a high cost), within-pond competition among tadpoles with an advantage for early and large tadpoles and finally factors relating to mate choice at the breeding site.

Introduction

In the study of life-history strategies, fundamental traits are the size and number of offspring. Also, the timing of breeding is an important characteristic that is often found to interact with the others. The characteristic is most easily studied in seasonal habitats and species with one 'explosive' breeding season. This is typically the case with many species of frogs (Wells, 1977) but similar issues arise in other groups and is a vast research field with, for example birds (Verhulst & Nilsson, 2008). It is usually assumed that earlier is basically better for the offspring and early breeding is balanced against parent capability or environmental risks. For example, older birds (Enoksson, 1993) and large frogs (Loman & Madsen, 1986; Tejedo, 1992) usually breed earlier. Early breeding in birds results in an increased risk of bad weather and poor feeding conditions for the young (Nilsson, 1994) and early spawning in temperate frogs increase the risk of cold weather and egg losses due to freezing (Frisbie, Costanzo & Lee Jr, 2000). The advantages of early breeding are usually assumed to show as a competitive edge when the fledglings become independent (Loman, 1984; Enoksson, 1993) or a large autumn size for frogs (Lyapkov *et al.*, 2000), increasing survival possibility during the first winter and

eventually a large clutch, characteristic of large individuals (Ryser, 1996).

With frogs, this reasoning carries the assumption that early breeding and egg laying also means early metamorphosis. Is this true and, if it is, how much of any time advantage during the early egg stage is really carried over to the metamorphosis? During the breeding time of many early temperate frogs, the water temperature is usually quite low, especially during night. Freezing ponds, with an ice cover, are not uncommon at this time. In Skåne, southern Sweden, maximum and minimum average air temperature in April is 12.0 and 3.6 °C, respectively (data for Lund 17 km from the site of the experiments). Frogs, being heterothermic, have a low metabolism and growth rate at this temperature. In contrast, when metamorphosis takes place in summer, the temperatures are much higher. In June, the corresponding temperatures are 20.2 and 11.6 °C. Development proceeds quicker at this temperature (Q10 rule, Nichelmann *et al.*, 1997).

Basically, at a constant pond temperature, one would expect tadpoles from early-laid eggs to metamorphose before tadpoles from late-laid eggs, with the time advantage being the same number of days as that between laying dates. Under natural conditions, with increasing water temperatures during the development period, this is not

necessarily so. Because water temperatures tend to increase as spring progresses, late tadpoles experience on average higher temperature and eggs develop faster at high than at low temperatures (Beattie, 1987; Laugen, Laurila & Merilä, 2003). One would therefore expect the metamorphosis interval at a pond to be shorter than the spawning interval (first laid to last laid egg). However, there is one more factor to take into account in the analysis of the consequences of date of breeding on metamorphosis time. This is the possibility of a genetic difference in developmental and growth rates. It is possible that eggs laid late differ genetically from those laid early; adaptations on the development rate may be present and may influence the pattern, in addition to the direct effects of water temperature. On a regional scale, Sparks *et al.* (2007) have suggested that an adaptive variation in the phenology (spawning time) of frogs (*Rana temporaria* and *Bufo bufo*) is present but I know of no study that explores this on a local scale.

The present study is aimed to explore these patterns. This is only a first step towards a fuller understanding; what 1, 2 or 10 days' difference in time for metamorphosis eventually means for winter survival and other aspects of fitness is beyond the scope of this study.

The study covers two separate periods in the frogs' (*R. temporaria*) development. I first analyse the egg period and then the larval period.

Methods

Effect of laying time – field study

In 1996, 1997 and 1998, I recorded the first date of laying for *R. temporaria* in a large number of ponds (53, 74 and 65, respectively) in Skåne, southern Sweden. Furthermore, in those ponds where there were several breeding sites, this was done for each site separately (in total 90, 118 and 105). I then recorded the time for first hatching of tadpoles at these sites. Ponds were visited approximately every 5 days and from the appearance of spawn and hatchlings, it was possible to estimate the laying and hatching date with an error of at most 2 days.

Egg survival in the field

Egg clutches of *R. temporaria* are usually placed at the water surface, and are exposed to the risk of freezing if the pond is covered by ice. To document an example of the costs associated with early laying, I took advantage of the temperature situation in April 2003. After the laying of the earliest *R. temporaria* clutches (28 March), there were freezing temperatures during six nights, the last on 9 April. On 10 April, I sampled seven clutches (spawn clumps). Four were from pond K, laid on 28 March, and three from another pond in the vicinity (Dalby hage, pond D), laid on 3 April. On 17 April, I sampled another eight clutches that were all laid after the last freezing night. Four were from pond K, laid on 11 April, and four were from pond D, laid on 12 April. After a few days, it was obvious which eggs were dead and these were all counted. The total number of eggs in the clutches was estimated by

weighing the full clutch, weighing a sample and counting the number of eggs in the sample. These samples contained between 22 and 68 eggs.

Effect of hatching time – experimental study

This study was conducted in 2003 and used *R. temporaria* eggs from two sites in Skåne. The eggs were hatched and tadpoles raised in outdoor tanks were placed at the Lund University field station Stensöffa (55°40'N, 13°30'E).

Eggs or newly (first day after hatching) hatched tadpoles were taken from Kungsmarken (pond K) (55°43'N, 13°17'E), which is a breeding site where eggs are laid typically among the earliest in the area but where also some late-laid eggs are usually found. In 2003, the earliest eggs in this pond were laid on 28 March and the latest on 15 April. Eggs were also taken from Vanstad (pond V) (55°35'N, 13°54'E), about 40 km further east. In this pond, eggs are typically laid quite late. In 2003, all eggs were laid on 18–20 April.

There were two sets of experiments. The 'natural delay study' (NDS) compares the development time of tadpoles from early- and late-laid clutches. The 'experimental delay study' (EDS) compares eggs from the same (early laid) clutch that were manipulated into two groups to hatch early or late. Both experiments come in two versions: short and long time delays.

For the NDS, early tadpoles were taken from six egg clumps at the Kungsmarken pond when they hatched on 15 April. Late-hatched tadpoles (short delay) were taken from six other clumps at Kungsmarken when these hatched on 21 April and (long delay) from six clumps at Vanstad when these hatched on 26 April. The newly hatched eggs were transferred to small containers with the algae-covered remains of egg jelly. This is typically used for food by newly hatched tadpoles. When the outer gill had disappeared, they were transferred to the large experimental tanks. This was 3–4 days after hatching.

For the EDS eggs were taken from six clumps at Kungsmarken 5 April. They were then transferred to a refrigerator at c. 6 °C and later in a greenhouse at approximately natural outdoor temperatures. By shuffling them back to the fridge, time for hatching could be adjusted. For the early tadpoles in both the short and the long time delay EDS, these tadpoles were adjusted to hatch on 15 April. For the short time delay EDS, late tadpoles were adjusted to hatch on 22 April and for the long delay EDS on 26 April.

Each of the four experiments (NDS short and long, EDS short and long) used six large tanks. The tanks contained 80 L water and a depth of c. 25 cm was maintained throughout the study. They were subdivided into two equal parts with a net with a 1.5 mm mesh size. In each tank I placed (on either side of the net) six 'early' and six 'late' tadpoles (Fig. 1). Each of these two groups contained one tadpole from each of six spawn clumps, same clumps for all six groups. For the EDS, the same six spawn clumps were used for the early and for both late groups. For the NDS, of course, different sets of spawn clumps, in all 18, were involved.

The tanks were filled with water and some dead leaves added for algae substrate already by the beginning of

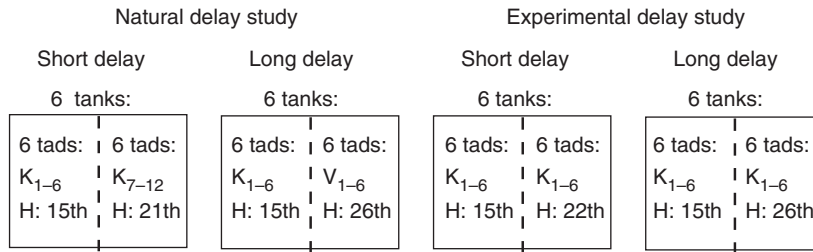


Figure 1 Overview of the experimental set-up. Rectangles represent tanks separated into two sections by a net (dashed line). K_A and V_A represent clutch numbers from Kungmarken and Vanstad, respectively. H is the date of hatching (day of April). There were in all 24 tanks with two sections each.

March. This means that by the time the tadpoles were introduced there were algae growing for food. The tanks and tadpoles were left alone; only some water filled during dry and hot weather periods until the time for metamorphosis approached. At that time, the tanks were monitored daily and all tadpoles with a tail <30% body length were removed. At this stage (Gosner 44), I recorded their body length and mass.

Results

Egg development and water temperature

The spring in 1996 was cold (Fig. 2) and breeding only began by the middle of April when temperatures quickly increased (Fig. 2). This resulted in a short breeding season. Actually, late-laid clutches that could not take advantage of the short period with very warm weather around 20 April sometimes developed slower than early ones! This year there was no significant effect of breeding date on egg development time. This was tested in an ANCOVA that accounted for pond effects (d.f. = 55,33, $F = 2.21$, $P = 0.008$) and entered breeding date as a covariate (d.f. = 1,33, $F = 0.109$, $P = 0.74$). Springs in 1997 and 1998 were warmer. Breeding had begun already by the end of March and proceeded much more gradually, and clutches were still laid as late as the end of April. In these 2 years it was very obvious that late-laid eggs needed a much shorter time to hatch (Fig. 2). The total development time was up to 30 days for those laid earliest and as short as 8 days for some late-laid eggs. There were significant effects of time of laying on development time in these 2 years (1997: d.f. = 1,43, $F = 64.7$, $P < 0.001$; 1998: d.f. = 1,28, $F = 29.8$, $P < 0.001$). The pond effects were significant in 1998 (d.f. = 65,28, $F = 1.86$, $P = 0.036$) but not in 1997 (d.f. = 73,43, $F = 1.12$, $P = 0.35$).

Egg survival

There was considerable variation in the survival of those eggs that had experienced nights with temperatures below 0 °C. Average egg survival was 79.6%, which was considerably less than that for eggs laid after the last night with sub zero conditions, 97.2% (t -test: d.f. = 6,9, $t = 4.1$, $P = 0.005$).

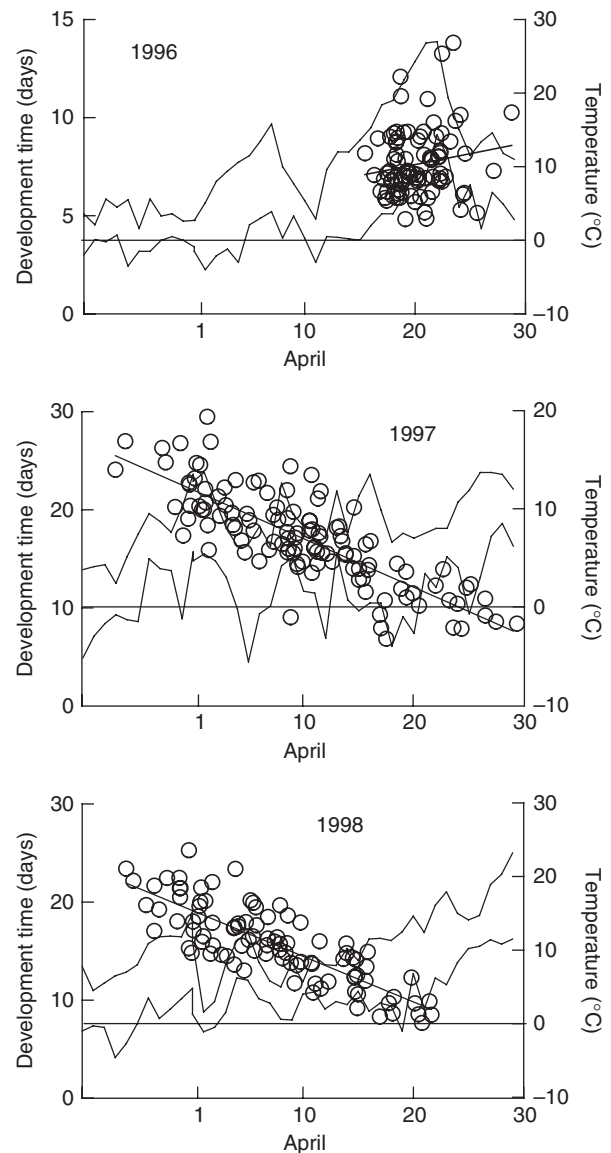


Figure 2 Effect of laying date on egg development time (left scale) in 3 years. This plot (open circles, left scale) shows overlaid graphs of daily maximum and minimum air temperatures (line, right scale). The horizontal line shows 0 °C.

Hatching delay and time for metamorphosis

Naturally late-hatched tadpoles in pond K (which hatched 6 days later than early tadpoles in the same pond) metamorphosed on average 2.4 days later (Table 1). Thus, they developed 3.6 days faster. Tadpoles from pond V (which hatched 11 days later than early tadpoles in pond K) metamorphosed on average only 1.9 days later and thus developed 9.1 days faster. When hatching was delayed experimentally (by 7 or 11 days) for some eggs in a clutch,

these tadpoles metamorphosed 1.9 and 5.1 days later, respectively. In all four cases, late tadpoles developed significantly faster than early hatching ones (Tables 1 and 2).

Size at metamorphosis

Naturally late-hatched tadpoles traded fast development for poor growth; in both cases they were significantly shorter (and in one case also lighter) than early tadpoles (Tables 1 and 2). Experimentally shortly delayed tadpoles were also smaller but the differences were less and not significant. In the other, long delay, experimental study, there was no size difference at all.

Table 1 Performance of tadpoles in the tadpole hatching delay studies

	Day of metamorphosis		Development time (days)	Body length (mm)		Body mass (g)	
	<i>n</i>	Mean		<i>n</i>	Mean	<i>n</i>	Mean
Natural delay							
6 days							
Early	27	8.7	54.7	26	10.6	26	0.123
Late	21	11.1	51.1	21	9.5	21	0.104
Difference		2.4					
11 days							
Early	21	9.6	55.6	20	10.8	18	0.13
Late	27	11.5	46.5	27	10	27	0.112
Difference		1.9					
Experimental delay							
7 days							
Early	21	11.1	57.1	21	10.5	21	0.121
Late	30	13	52	29	9.9	29	0.113
Difference		1.9					
11 days							
Early	29	11.4	57.4	28	10.3	28	0.128
Late	22	16.6	51.6		10.4	28	0.13
Difference		5.2					

Day of metamorphosis is date in June. *N* is the number of tadpoles measured; with 100% survival this had been 36 for all sets.

Natural versus experimental hatching delay

When spawn from only pond K was used (the 6/7 days delay studies), the development rates of both late groups were similar; naturally late hatched took 51 days and experimentally late hatched took 52 days to develop. However, eggs experimentally delayed by 11 days from pond K developed slower than tadpoles from the 'late' pond V that naturally hatched at the same time. The former needed 52.0 days for development while the latter metamorphosed after only 46.5 days (Table 1). This difference is significant (two-way ANOVA with tank (6 + 6) nested under treatment (natural/artificial); $F = 8.7$, d.f. = 1,37, $P = 0.006$).

Discussion

Possible bias and errors

I recorded egg development time in the field as the time from the date of first laying at a site to that of first hatching at the same site. I think it is safe to assume that some of the first laid eggs were among some of the first to hatch at the site. Thus, the measure correctly records the development time

Table 2 Tests for an early/late effect on the dependent variables in Table 1

	Development time (days)			Body length (mm)			Body mass (g)		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Natural delay									
6 days									
Early versus late	54.9	1,41	<0.001	10.35	1,40	<0.001	6.98	1,41	0.012
Tank	3.31	5,41	0.013	1.17	5,40	0.34	2.73	5,41	0.032
11 days									
Early versus late	72.2	1,41	<0.001	8.69	1,40	0.005	3.42	1,38	0.072
Tank	1.74	5,41	0.15	1.77	5,40	0.14	1.61	5,38	0.18
Experimental delay									
7 days									
Early versus late	11.5	1,44	<0.001	1.87	1,43	0.120	0.26	1,43	0.61
Tank	3.55	5,44	0.009	1.54	5,43	0.20	0.96	1,43	0.46
11 days									
Early versus late	5.22	1,44	0.027	0.16	1,43	0.660	0.25	1,43	0.62
Tank	2.37	5,44	0.054	4.34	5,43	0.001	8.70	5,43	<0.001

The effect is tested with a two-way ANOVA, analyzing in addition to the early/late effect also tank effects, which is a confounding variable.

for some eggs at the site. However, the measure is not without its complications. If there is a variation in development time, the average clutch development time at the site may well be longer. However, there is no reason to suspect that this error is biased with respect to the time of season. Also, there is one phenomenon that errs it in the opposite direction. Late breeding females have the option to place their clutches in the middle of the spawn aggregation at the breeding site. Because this placement is favourable from a temperature point of view, these clumps develop somewhat faster than those in the periphery (Loman & Håkansson, 2004). Furthermore, most breeding at a site took place during a quite short time span (median 2 days). The time advantage for central spawn was also rather limited (about 2 days). I thus think the measure used has sufficient precision to prove the point of the present study.

All tadpoles did not survive in the tank. This could affect development time, reducing it in tank sections with fewer survivors. To control for this, I conducted preliminary tests with number of surviving tadpoles as a covariate. However, this factor never turned out to be significant and *P* values for the remaining factors (tank and hatching time) were only marginally changed by inclusion of this covariate. It was thus removed from the final tests as shown in Table 2.

Interpretation

Basically, early time delays are maintained but reduced at the time of hatching and metamorphosis. This is as expected from seasonal pond temperature patterns and the progressive temperature effects on development time in ectotherms. However, it seems that the advantage of early egg laying varies among years, depending on the particular pattern of spring temperature development. In years with an early spring and/or a gradual increase in temperature, breeding is extended and there may be up to a 30-day difference between early- and late-laid eggs but less so between early and late-hatched eggs. The most extreme year in my study was 1997. Early eggs were laid on 24 March and hatched on average 20 April. Late eggs were laid as much as 35 days later but hatched only 16 days later (from Fig. 2).

This observational egg study does not account for any genetic effect. It is quite possible that frogs that 'chose' to breed late have eggs that develop quicker. Laugen *et al.* (2003) have shown that egg development time has a genetic component. Further studies are needed to evaluate this possible pattern. However, it seems unlikely that late eggs should develop more than twice as fast for purely genetic reasons. Most of the difference in development time is thus likely due to the average warmer water experienced by late-laid eggs, at least in some years.

The tadpole experimental delay study (EDS), however, controls for genetic effects. It shows that although late-hatched tadpoles also hatch late, they develop faster. In this case, a 7- or an 11-day head start shrunk to 2 and 5 days, respectively, at hatching time. The shorter development time is what one would expect when taking the average higher temperature into account.

The result was similar (2 days later metamorphosis) in the tadpole natural delay study (NDS) with a 6-day hatching delay. This suggests that the development rate genotype was similar for tadpoles from early- and late-hatched (and thus laid) eggs in a given pond (in this case pond K). However, in the NDS with a long time interval, late-hatched tadpoles (from pond V, with all naturally late breeding) developed faster than experimentally delayed tadpoles (hatching on the same day as those from pond K) from the pond with average early hatching (pond K). Tadpoles from these two ponds may thus differ genetically in the development rate. Combining this effect and temperature effects, tadpoles from pond V, hatching 11 days later than the early ones from pond K, metamorphosed only 2 days later!

The suggestion that genetically influenced strategies are involved is supported by the metamorph size effects. In the EDS the growth and development process was merely delayed and contracted, likely due to the higher average temperature; metamorphosis took place at the same size for early and late tadpoles alike. The even higher development rate for naturally late tadpoles came, on the other hand, at a cost; they were smaller at metamorphosis. This pattern and interpretation is not fully valid for the shorter delay studies, though.

Also maternal effects may be involved. It is known that the average egg size differs among ponds (Loman, 2001a), and tadpoles from large eggs tend to metamorphose early (Loman, 2002).

Other studies

Reading & Clarke (1999) report findings similar to mine for development of toad *B. bufo* eggs and tadpoles. However, they compared the egg development time among different years. In the years when toads bred early, total egg and tadpole development was much longer than in late years. In this case, the among-year span in breeding date was almost 2 months but early breeding resulted in a metamorphosis only about 1 month earlier than that in late years. In contrast to this, Berven (1990), studying *Rana sylvatica*, a species with a breeding ecology very similar to *R. temporaria*, however, did not find a correlation between early breeding and long development.

Consequences and causes of variation in phenology

Why do frogs breed early and risk reduced survival of eggs if freezing weather should strike after egg laying? As the present study shows, cold weather, which is not uncommon at this time of the year, could cause substantial egg mortality. Delaying breeding by 2 weeks may decrease this risk and likely only results in 1 week later hatching and at the time of metamorphosis only a few days' delay. There are several possible explanations for this behaviour.

After all, a few days earlier metamorphosis at a given size may be critically important for the future survival and fitness. This should result in a higher autumn size, which is important for winter survival (Smith, 1987; Lyapkov, 1997; Altwegg & Reyer, 2003).

A direct effect of season on tadpole growth and survival is also possible. It could be that food is more plentiful or of a higher quality early in the season. In this category of explanations effects of competition with other organisms should also be included, for example, snails (Loman, 2001*b*). Such effects have indeed been suggested for *Rana japonca* (Matsushima & Kawata, 2005) and *Hyla andersoni* (Morin, Lawler & Johnson, 1990). In these studies, early hatching tadpoles survived better than late.

Another class of explanations relates to the possibility of intra-specific within-pond competition. This could drive a selection for early breeding. Interference competition among metamorphs and young frogs should tend to increase the advantage for early metamorphosis and cannot be dismissed but seems far fetched. The situation is different with newly hatched tadpoles. During their first days of life, the tadpoles appear to feed on algae growing on the disintegrating jelly that has coated the eggs. In this situation, tadpoles feed at very high densities and interference competition seems quite likely. Also, the resource is possibly exhausted by the earliest hatching tadpoles. This may leave those tadpoles that hatch last at a breeding site in a poorer position than earlier ones. The situation is made more complicated by the fact that late-breeding females have the option of putting their spawn in a central and temperaturewise more favourable position than the earliest one (Loman & Håkansson, 2004). Nonetheless, it seems here is a possibility for a disadvantage for late breeders. Also, among older tadpoles, competition is possible. Effects of intra-specific tadpole competition have indeed been documented (Loman, 2001*c*, 2004). Also, tadpoles cannibalizing eggs and younger tadpoles (Petranka & Thomas, 1995) are a cause for early and breeding.

It is also possible that early breeding is not at all related to egg and tadpole growth and survival but rather an effect of competition for good mates. In frogs with explosive breeding active female choice is less likely to be important than male choice (Berven, 1981; Halliday, 1983). However, by being present on the male competition arena a passive female choice is possible (Davies & Halliday, 1979). A late arriving female may be less likely to take advantage of male–male competition to secure mating from a genetically more fit male. Arriving early, securing a preferred mate but delaying oviposition is an option, but implies a substantial risk of predation at the breeding site (Lodé, 2000; Benard, 2007). It may be better for a female to arrive early and spend as short a time as possible at the breeding site. Early breeding may be related to mate choice strategies.

The present study provides no clues to a choice among these alternatives; it merely highlights the problem.

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References

- Altwegg, R. & Reyer, H.-U. (2003). Patterns of natural selection on size at metamorphosis in water frogs. *Evolution* **57**, 872–882.
- Beattie, R.C. (1987). The reproductive biology of common frog (*Rana temporaria*) populations from different altitudes northern England. *J. Zool. (Lond.)* **211**, 387–398.
- Benard, M. (2007). Predators and mates: conflicting selection on the size of male pacific treefrogs (*Pseudacris regilla*). *J. Herpatol.* **41**, 317–320.
- Berven, K. (1981). Mate choice in the wood frog, *Rana sylvatica*. *Evolution* **35**, 707–722.
- Berven, K. (1990). Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* **71**, 1599–1608.
- Davies, N.B. & Halliday, T.R. (1979). Competitive mate searching in male common toads, *Bufo bufo*. *Anim. Behav.* **27**, 1253–1267.
- Enoksson, B. (1993). Effects of female age on reproductive success in European nuthatches breeding in natural cavities. *Auk* **110**, 215–221.
- Frisbie, M.P., Costanzo, J.P. & Lee, R.E. Jr (2000). Physiological and ecological aspects of low temperature tolerance in embryos of the wood frog, *Rana sylvatica*. *Can. J. Zool.* **78**, 1032–1041.
- Halliday, T. (1983). Do frogs and toads choose their mates? *Nature* **306**, 226–227.
- Laugen, A.T., Laurila, A. & Merilä, J. (2003). Latitudinal and temperature-dependent variation in embryonic development and growth in *Rana temporaria*. *Oecologia* **135**, 548–554.
- Lodé, T. (2000). Functional response and area-restricted search in a predator: seasonal exploitation of anurans by the European polecat, *Mustela putorius*. *Aust. Ecol.* **25**, 223–231.
- Loman, J. (1984). Breeding success in relation to parent size and experience in a population of the hooded crow *Corvus corone cornix*. *Ornis Scand.* **15**, 183–187.
- Loman, J. (2001*a*). Local variation in *Rana temporaria* egg and clutch size – adaptations to pond drying. *Alytes* **19**, 45–52.
- Loman, J. (2001*b*). Effects of tadpole grazing on periphytic algae in ponds. *Wetl. Ecol. Manage.* **9**, 135–139.
- Loman, J. (2001*c*). Intraspecific competition in tadpoles, does it matter in nature? A field experiment. *Popul. Ecol.* **43**, 253–263.
- Loman, J. (2002). Microevolution and maternal effects on tadpole *Rana temporaria* growth and development. *J. Zool. (Lond.)* **257**, 93–99.
- Loman, J. (2004). Density regulation in tadpoles *Rana temporaria*: a full pond field experiment. *Ecology* **85**, 1611–1618.
- Loman, J. & Håkansson, P. (2004). Communal spawning in the common frog *Rana temporaria* – egg temperature and predation consequences. *Ethology* **110**, 665–680.

- Loman, J. & Madsen, T. (1986). Reproductive tactics of large and small male toads *Bufo bufo*. *Oikos* **46**, 57–61.
- Lyapkov, C.M., Cherdantsev, V.G., Cherdantseva, Y.M. & Severtsov, A.S. (2000). Survival and growth of brown frog juveniles dispersing from breeding pond. *Entomol. Rev.* **80** (Suppl. 1), 167–180.
- Lyapkov, S.M. (1997). Peculiarities of growth in *Rana temporaria* and *Rana arvalis* in the first years of terrestrial life. Influence of size on survival during wintering. *Zool. Zhur.* **76**, 356–363.
- Matsushima, N. & Kawata, M. (2005). The choice of oviposition site and the effects of density and oviposition timing on survivorship in *Rana japonica*. *Ecol. Res.* **20**, 81–86.
- Morin, P.J., Lawler, S.P. & Johnson, E.A. (1990). Ecology and breeding phenology of larval *Hyla andersoni*: the disadvantages of breeding late. *Ecology* **71**, 1590–1598.
- Nichelmann, M., Tzschentke, B., Basta, D., Burmeister, A. & Janke, O. (1997). Q10 in perinatal thermoregulation. In *IIIrd International workshop on investigations of perinatal development in birds*: 211–223. Tönhardt, H. & Lewin, R. (Eds). Berlin: Frei Universität Berlin.
- Nilsson, J. (1994). Energetic bottle-necks during breeding and the reproductive cost of being too early. *J. Anim. Ecol.* **63**, 200–208.
- Petranka, J.W. & Thomas, D.A.G. (1995). Explosive breeding reduces egg and tadpole cannibalism in the wood frog, *Rana sylvatica*. *Anim. Behav.* **50**, 731–739.
- Reading, C.J. & Clarke, R.T. (1999). Impacts of climate and density on the duration of the tadpole stage of the common toad *Bufo bufo*. *Oecologia* **121**, 310–315.
- Ryser, J. (1996). Comparative life histories of a low- and a high-elevation population of the common frog *Rana temporaria*. *Amphibia-Reptilia* **17**, 183–195.
- Smith, D.C. (1987). Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* **68**, 344–350.
- Sparks, T., Tryjanowski, P., Cookje, A., Crick, H. & Kuzniak, S. (2007). Vertebrate phenology at similar latitudes: temperature response differs between Poland and the United Kingdom. *Climate Res.* **34**, 93–98.
- Tejedo, M. (1992). Effects of body size and timing of reproduction on reproductive success in female natterjack toads (*Bufo calamita*). *J. Zool. (Lond.)* **228**, 545–555.
- Verhulst, S. & Nilsson, J.-A. (2008). The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos. Trans. Roy. Soc. Lond. Ser. B Biol. Sci.* **363**, 399–410.
- Wells, K.D. (1977). The courtship of frogs. In *The reproductive biology of Amphibians*. Taylor, D.H. & Guttman, S.I. (Eds). New York: Plenum Publishing Corp.