WHEN CROWDED TADPOLES (*RANA ARVALIS* AND *R. TEMPORARIA*) FAIL TO METAMORPHOSE EARLY AND THUS FAIL TO ESCAPE DRYING PONDS

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Do moor frog (*Rana arvalis*) and common frog (*R. temporaria*) tadpoles increase developmental rate if there is a risk of their pond drying up before metamorphosis? To study this, I performed an experiment designed to mimic natural conditions in many drying ponds. The number of tadpoles per tank was constant during the experiment but the water level was lowered in experimental tanks so that crowding increased. Experimental tadpoles grew and developed more slowly than control tadpoles that were in constant water volume. Also, metamorphosis was delayed (i.e. a smaller proportion had metamorphosed when the experiment was concluded on 1 August) and the metamorphs were smaller. I conclude that, due to crowding, the tadpoles in this experiment were not able to speed up development rate adaptively. Performance of the tadpoles in the experiment was compared to that of *R. temporaria* tadpoles in the field. These lived in a pond where desiccation resulted in division of the water body into a small pool and a large pool. The small pool dried out completely before the rest of the pond. Tadpoles in this pool were smaller and had relatively smaller hind legs, suggesting slower development. This pattern confirms the result of the experiment, supporting my suggestion that the experimental set-up mimicked many natural situations. Of particular interest is the fact that other studies – carried out both in the same geographical area and elsewhere – have shown *R. temporaria* to have the ability to respond adaptively to pond drying. The fact that it did not do so in this particular experiment, as well as in the field pond studied here, shows that care must be exercised when extrapolating from one study to the properties of a species. Different conditions, both in the field and in experiments, may well give different responses.

Key words: amphibian development, competition, frog tadpoles, drying ponds

INTRODUCTION

Ponds used by breeding frogs range from permanent waters to temporary. In dry years, frogs breeding in temporary ponds face the risk of losing all offspring (Wilbur, 1984; Semlitsch & Wilbur, 1988; Tejedo & Reques, 1994, Griffiths, 1997; Barandun & Reyer, 1997). This habitat is used by many aquatic organisms that have evolved various strategies to survive (Wiggins, Mackay & Smith, 1980). Strategies to counter the risk of pond desiccation should be under strong selective pressure.

A facultative shortening of development time would be one such strategy suitable for frogs. This is likely to involve a trade-off between early metamorphosis at a small size and late metamorphosis at a large size (Merilä *et al.*, 2000*b*). The optimum balance may depend on information concerning the quality of the breeding pond (including expected hydroperiod) as well as the expected quality of the future terrestrial habitat (Wilbur & Collins, 1973; Werner, 1986). Plasticity in timing of metamorphosis has indeed been demonstrated for amphibians in experiments by Semlitsch & Wilbur (1988) for *Ambystoma talpoideum*; Crump (1989) for *Hyla pseudopuma*; Newman (1989) for *Scaphiopus couchii*; Tejedo & Reques (1994) for *Bufo calamita*; and Laurila

& Kujasalo (1999) for *Rana temporaria*. A pattern of size at metamorphosis and time to metamorphosis in the field that supports this plasticity has been demonstrated for a salamander *Ambystoma talpoideum* (Semlitsch *et al.*, 1988). Extreme plasticity has been demonstrated in *Scaphiopus hammondii* tadpoles that were not only able to accelerate development as water levels decreased but were also able to slow development when water levels were raised again (Denver, Nooshan & Phillips, 1998). A similar level of plasticity in mosquitoes has also been shown (Juliano & Stoffregen 1994). In contrast to the studies above, tadpoles of the *Rana esculenta* complex did not exhibit a plastic response in time to metamorphosis when exposed to experimental pond drying (Semlitsch & Reyer, 1992).

Growth rate and developmental rate both tend to increase with decreased competition, as shown by Wilbur (1976; 1977*a*) and modelled by Hentschel (1999). This is likely to be an effect of increased food resources. Thus, such responses are not necessarily adaptive. Growth rate and development rate are not necessarily coupled but may respond to different cues (Smith-Gill & Berven, 1979). If tadpoles in drying ponds accelerate developmental rate, this may proximately be due to tadpoles somehow directly sensing the decrease in water level. Alternatively, tadpoles may sense increased competition and respond to this, either because it is an indication of a dangerously decreasing water volume or because in itself it constitutes an adverse condition, mo-

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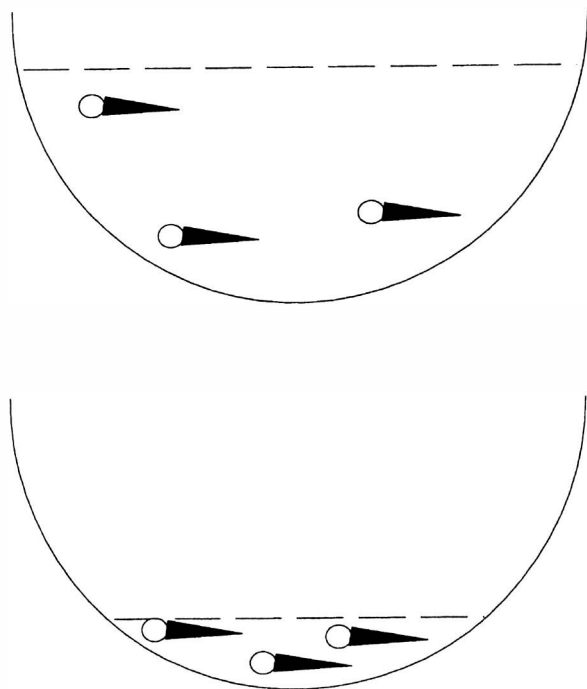
FIG. 1. Cross section of the experimental tanks. Decreasing water level not only reduces water volume but also substantially reduces the area available for algal growth.

TABLE 1. Manipulation of water volume (litres) in tanks with different water reduction schemes. "Dry 1", "Dry 2" and "Dry 3" are considered experimental tanks.

	Start	Day of treatment			
	23 April	7 May	21 May	5 June	17 June
Control	80	80	80	80	40
Dry 1	80	40	20	10	5
Dry 2	80	20	10	5	2.5
Dry 3	80	10	5	2.5	1.25

tivating a quick escape onto land. Both these responses are adaptive (Gotthard & Nylin, 1995) and only differ in proximal cues.

In Sweden, breeding ponds used by *Rana arvalis* (moor frogs) and *R. temporaria* (common frogs) are variable in terms of the risk of drying. Many frogs breed in ponds that contain adequate water in most years but that do dry in some years, causing catastrophic mortality. Thus, drying of a pond is a mortality factor of some importance for tadpoles of these species (Cooke, 1985; Kutenkov & Panarin, 1995; Loman, 2001). The present study is an attempt to investigate wheter *R. arvalis* and *R. temporaria* exhibit plasticity with respect to developmental rate.

This study has two parts. The first is an experiment where manipulation of water level was done in large tanks. Water level was decreased without any change of tadpole numbers. Due to the shape of the tanks, this also reduced the area available for algal growth and thus led to reduced resources (Fig. 1). Any effects on development rate could thus have been due either to effects of crowding (combined with reduction of resources) or to direct responses (if so, presumably adaptive) to decreased water level. This treatment should mimic a natural pond with little mortality. The second part is a field study of a shallow natural pond. During spring and early summer, part of the pond was naturally cut off and dried out more quickly than the main basin. Performance of tadpoles in the two parts of the pond were compared and results compared to those of the experiment.

MATERIALS AND METHODS

COLLECTION AND INTRODUCTION OF TADPOLES

Newly hatched tadpoles (not more than two days old) were collected during April 1990 from four breeding ponds; two with *R. arvalis* and two with *R. temporaria*. They were situated within 20 km of each other in the province of Skåne in southernmost Sweden. The samples contained tadpoles from several clutches at each pond. After collection, all tadpoles from one site were mixed. After two days (when their condition had been monitored and any weak or dead individuals replaced), on 23 April, tadpoles were introduced into 20 tanks. At the start of the study there were 80 tadpoles in each tank. All tadpoles in one tank were from the same pond.

TANKS

The 20 tanks were located outdoors at Lund University Ecology Department's field station, 17 km east of Lund (55° 40' N, 13° 30' E). They were made from 200 litre plastic barrels, cut in half lengthwise. Two weeks before the introduction of the tadpoles, tanks were filled with 80 litres of tap water and "inoculated" with about 2 litres of pond water. Some vegetation (strings of *Elodea canadensis*, *Ranunculus aquatilis*, and *Chara* sp.) was added to ensure an adequate oxygen level in the tanks. No more food was added. Tadpoles fed exclusively on resources produced in the tank; mainly algae growing on vegetation and on the wall of the tank. Tanks were covered with lids of fine mesh netting to prevent colonization by predaceous insects. Above the tanks I suspended a thin layer of textile material to provide shading from the sun. This reduced temperature extremes.

EXPERIMENTAL DESIGN AND ANALYSIS

The two species were sampled in different ponds and each housed in 10 tanks. Of these ten tanks, four were control tanks (two from each pond) and six experimental (three from each pond). The effects of source pond and species were not within the scope of the study. These effects had the nature of blocking factors and

were included as factors in the tests, but the effects of species and pond *per se* were not further considered. Testing tadpole performance (variables in Table 3), mean measurements for each tank were used as data for dependent variables. Testing metamorphosis success, percentage metamorphosing in each tank (Table 2, "% metam.") was used as data for the dependent variable. Some tadpoles were lost. Lost tadpoles (dead or possibly escaped as metamorphs) were excluded from the total when computing the percentage metamorphosing. In tanks with reduced water, depth was at most 5 cm during the period of metamorphosis. In these tanks all tadpoles were clearly visible and any lost tadpoles could be attributed to mortality. In the control tanks, water level was always at least 20 cm and, as visibility in some of the tanks was reduced due to algal blooms, some of the lost tadpoles may have reached metamorphosis unnoticed and escaped. For this reason, control tanks were not used for analysis of survival.

EXPERIMENTAL TREATMENTS OF WATER LEVEL

Two control tanks from each pond (i.e. eight tanks in total) had constant water levels almost throughout the experiment. Only towards the end of the experiment was the water reduced to 40 litres. This reduction was made to facilitate the capture of metamorphs. In 12 experimental tanks, the water level was successively lowered to mimic a drying pond. The water in these tanks was lowered according to three different schemes; "Dry 1", "Dry 2" and "Dry 3" (Tables 1, 2). Three degrees of drying regime were used to guard against threshold effects. The full results are shown in the figures, but for statistical analysis a conservative approach was chosen and all three levels pooled. An exception is the analysis of lost (dead) tadpoles. Because the control tanks were not used, the three degrees of water reduction were contrasted in this analysis.

TADPOLE DENSITIES

Tadpoles that died during the course of the experiment were not replaced. However, on 30 May – when all tadpoles were counted (and measured) – few were missing. The tank with the highest mortality actually contained 71 tadpoles out of the original 80 (Table 2). The experiment was terminated on 1 August. All remaining tadpoles were counted (Table 2).

TABLE 2. Summary of the material used in the study. *R. a., Rana arvalis; R. t., Rana temporaria.* 'Dry', water level reduction scheme (1, moderate; 2, medium; 3, drastic). 'P', Original pond. On 30 May the tadpoles were measured. The experiment was concluded on 1 August when all remaining tadpoles were counted and measured. 'Lost' represents tadpoles dead since the last count of numbers as well as possible escapes of metamorphs. '% metam.' is the percentage recorded metamorphosing of all tadpoles that were present at the count on 30 May and not later lost.*/ Metamorphs in these two tanks were difficult to find due to algal blooms. Most of the lost tadpoles may have escaped.

Species	Treatment	Dry	P	Initial number	30 May Found	1 August Metamorphs found	Remaining tadpoles	% metam.	Lost
R. arvalis									
	Control		A	80	80	28	49	36.4	3
			A	80	78	29	42	40.8	7
			B	80	78	61	3	95.3	14
			B	80	78	67	5	93.1	6
	Reduced water	1	A	80	77	18	54	25.0	5
		1	B	80	78	65	4	94.2	9
		2	A	80	77	3	47	6.0	27
		2	B	80	71	52	6	89.7	13
		3	A	80	77	2	24	7.7	51
		3	B	80	74	28	22	56.0	26
R. temporaria									
	Control		C	80	78	19	0	100.0	59 */
			C	80	80	52	0	100.0	28 */
			D	80	78	60	9	87.0	9
			D	80	79	55	17	76.4	7
	Reduced water	1	C	80	80	59	0	100.0	21
		1	D	80	78	54	14	79.4	10
		2	C	80	76	36	19	65.5	21
		2	D	80	80	35	21	62.5	24
		3	C	80	75	46	20	69.7	9
		3	D	80	74	29	23	55.8	22

TABLE 3. Testing effects of treatments on tadpole performance. This was done with a 3-way hierarchical ANOVA. The factors included were treatment, species and pond (nested under species). All interactions were non significant and removed before final test. Data are average values for tanks.

	Treatment			Species			Pond		
	df	F	P	df	F	P	df	F	P
Tadpoles - body length	1,15	14.51	0.002	1,15	2.59	0.13	2,15	6.91	0.007
Tadpoles - leg development	1,15	3.74	0.072	1,15	0.03	0.86	2,15	22.8	<0.001
Metamorphs - body mass	1,15	18.38	0.001	1,15	0.05	0.83	2,15	2.13	0.1

EXPERIMENTAL PROCEDURES

The first experimental reduction of water level (on 7 May) took place when tadpoles were about two weeks old. This was early in development and the tadpoles had no visible limb buds, or early limb buds only (Gosner stage 25 to 27; McDiarmid & Altig, 1999). This was designated the start of the experiment, as prior to this date the tanks only served to house the growing tadpoles.

Therefore, to minimize any variation that was due not to the experimental treatments but to random tank effects, the following procedure was used on 7 May. The tadpoles were removed from the tanks and all 400 tadpoles (i.e. five tanks containing 80 tadpoles each) from one source pond were sorted into three or four size classes. One fifth of the tadpoles from each size class was assigned at random to each of the five tanks and reintroduced. The same procedure was repeated for each of the four pond-specific tank sets. Thus, tanks with tadpoles of the same species and source ponds started the experimental phase with samples of similarly sized tadpoles.

MEASUREMENTS

On 30 May all tadpoles were measured alive and returned to the tanks. Measurements taken were body length (snout-vent) and hind leg length. The latter was used to calculate "relative leg length" – leg length divided by body length. This was considered a measure of development rate; a tadpole with longer legs for its size being closer to metamorphosis.

The first metamorphs appeared on 17 June (*R. temporaria*) and 20 June (*R. arvalis*) respectively. After this, tanks were checked at least every other day. Tadpoles that had a tail shorter than body length were close to metamorphosis and were removed, weighed, and had their body length measured.

FIELD DATA

In 1995, tadpoles of *R. temporaria* were also collected in the field. This was from a pond, part of which had been naturally isolated due to a decreased water level following a dry spring. The two parts of the pond separated completely on 30 May, when the tadpoles were about five weeks old. The smaller and shallower part dried completely on 22 June, the larger (and deeper) part dried on 2 July. No tadpoles survived in either part of the pond that year. Tadpoles were collected from the smaller pool and from the main body of water on both 6 June and 20 June. Total area of the pond was about 500 m² at the time of spawning, and about 300 m² when the smaller pool (about 10 m²) was separated. Collected tadpoles were humanely killed and preserved, and body length and hind leg length were measured. Relative hind leg length (hind leg/body length) was used as an index of development.

RESULTS

EXPERIMENTAL TREATMENT

Tadpoles in tanks with reduced water were significantly smaller than those in control tanks (Fig. 2, Table 3). These tadpoles also had a tendency to have less developed hind legs on 30 May (Fig. 3, Table 3). Out of the tadpoles that did metamorphose, those from control tanks were larger than those from experimental tanks (Fig. 4, Table 3).

In control tanks, more tadpoles had metamorphosed by the time the experiment was concluded on 1 August than in the tanks with reduced water (Fig. 5, Table 2). The effect of treatment was significant (three-way
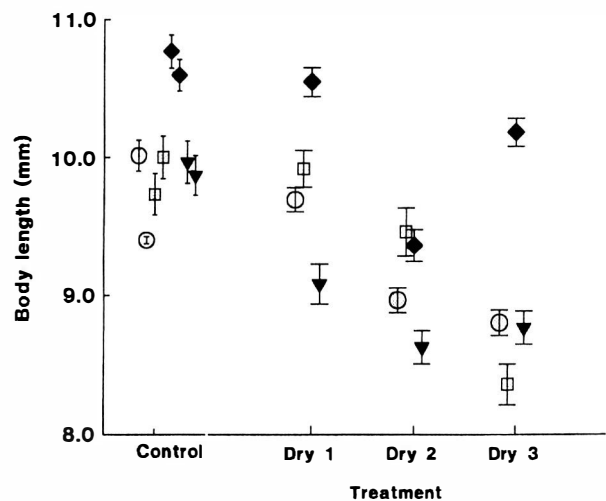

FIG. 2. Body lengths of tadpoles from different treatments. For each tank, mean length is given and standard error of mean indicated by the error bars. Number of measurements for each tank is given by Table 2. The four different symbols represent different source ponds. Open symbols are for *Rana arvalis* and filled symbols for *R. temporaria.*
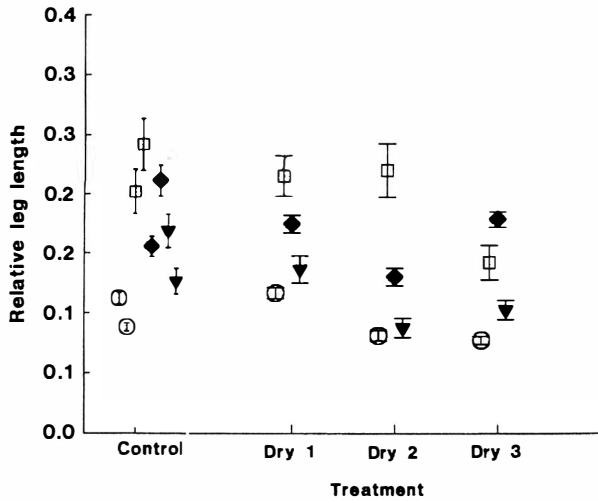
FIG. 3. Relative leg lengths (hind leg length/body length) for tadpoles from different treatments. Symbols as for Fig. 2.
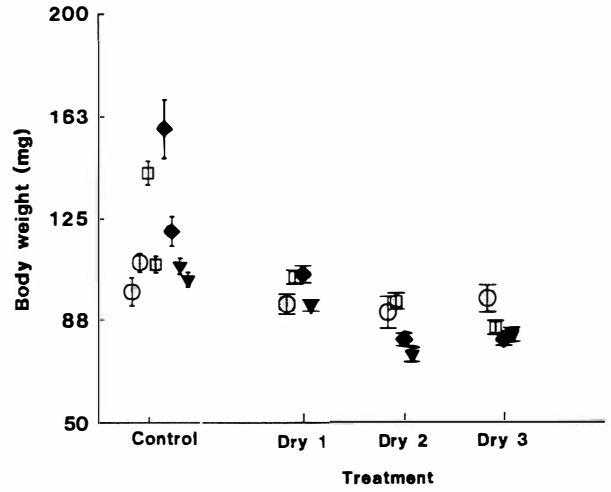

FIG. 4. Body weights of metamorphs from different treatments. Symbols as for Fig. 2.

ANOVA, controlling for species and pond (nested under species): $F=11.73$, df$=1,15$, $P=0.004$). For none of the above variables was there an interaction between species and treatment effects (all $P>0.25$). For *R. arvalis*, the proportion dead increased with the severity of drying (Fig. 6, two-way ANCOVA, $F=14.2$, df$=1,3$, $P=0.036$). Variation between ponds was not significant ($F=2.67$, df$=1,3$, $P=0.20$). There was no treatment effect for *R. temporaria*. The difference in slope between the two species was significant (three-way ANCOVA with species, pond [nested under species] and treatment, $F=6.81$, df$=1,6$, $P=0.040$).

FIELD DATA

R. temporaria tadpoles from the smaller and shallower part of the pond were smaller than those found in the rest (Table 4). Also, tadpoles from the small shallow part had less – developed hind legs. These results were true for both sampling periods.

DISCUSSION

Tadpoles subject to drying seemed to develop more slowly than those in control tanks. This is indicated by the tendency for such tadpoles to have more slowly developing legs. Also, few of the surviving tadpoles in the experimental tanks had metamorphosed before the end of the experiment compared to those in the control tanks. This conclusion is valid regardless of the undecided fate of the lost tadpoles in the control tanks. If they had died, the conclusions refer to surviving tadpoles in all tanks. If they had escaped, they should be added to those metamorphosing before 1 August, making the case even stronger. Extrapolating the tendency that fewer (*R. arvalis*) – or similar (*R. temporaria*) – numbers died in tanks with moderate water reduction compared to the control tanks, suggests that most of the large number lost in two such tanks were actually escapes. Also, the conclusion that metamorphs in experimental tanks were
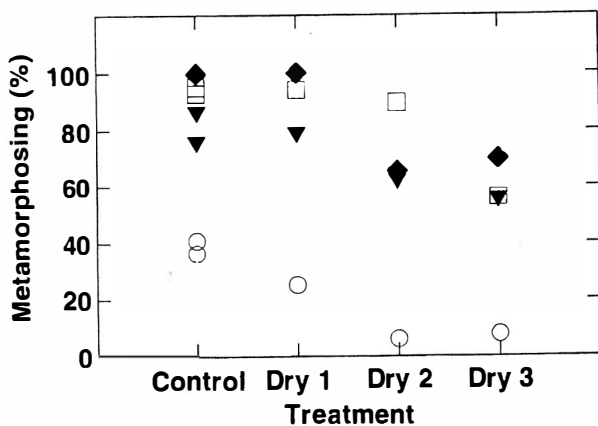

FIG. 5. Proportions of all tadpoles that metamorphosed before 1 August in the different treatments. Proportions based on all metamorphs found and all remaining tadpoles on 1 August. Symbols as for Fig. 2.
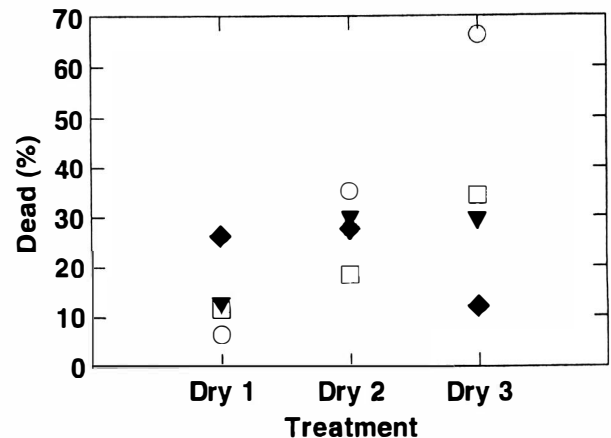

FIG. 6. Proportions of tadpoles that died in the different treatments. Control tanks were excluded because some of the lost tadpoles in these may have escaped rather than died. Symbols as for Fig. 2.

TABLE 4. Comparison of the performances of *Rana temporaria* tadpoles sampled from two parts of a natural drying pond.

	Deep part	Shallow part	t	P
Body length (mm)				
6 June	10.7 (*n*=39)	7.5 (*n*=8)	7.1	<0.001
20 June	12.3 (*n*=17)	8.6 (*n*=8)	7.3	<0.001
Relative hind leg length				
6 June	11 % (*n*=39)	6.0 % (*n*=8)	4.0	<0.001
20 June	24.4 % (*n*=17)	9.3 % (*n*=8)	4.4	<0.001

smaller is robust with respect to the problem of lost tadpoles. There is no reason to expect a size bias with respect to escaped tadpoles; all measures of metamorphs – in control and experimental tanks alike – are thus an unbiased measure of the size of tadpoles that had metamorphosed by 1 August. The measures of tadpoles were unaffected by the losses after 30 May. Before that, all losses were small and due to mortality. Effects found on tadpole size were thus not affected by mortality and escapes.

This effect of drying on development rate is contrary to what would be expected if tadpoles modified development rate adaptively and attempted to escape a drying
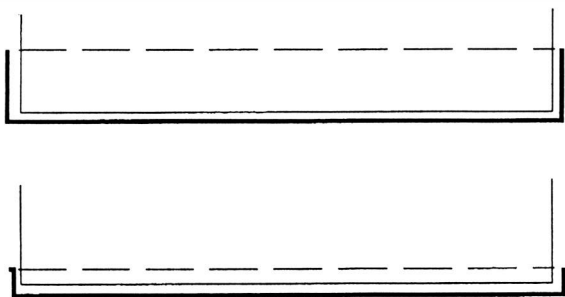
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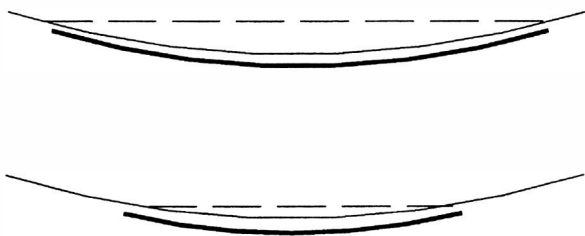
B

FIG.7. Effects from drying on pond bottom area in two types of pond. A, in ponds with sloping sides, drying results in less area available for tadpole feeding. B, in ponds with steep slopes, drying and reduction of water level may have small effects on the area available for feeding. Although tadpoles may be crowded by volume, the effects on resources per tadpole are small.

pond. It is also contrary to what is expected if the method used led to a higher temperature in the shallow experimental tanks. The result is thus not caused by a temperature bias. Because these tadpoles not only developed but also grew more slowly, they may simply not have reached the minimum size required for metamorphosis early enough to leave the water by the time the control animals metamorphosed. This supports the notion of a minimum size, as proposed by the model of Wilbur & Collins (1973). However, because those slow-growing experimental animals that did indeed metamorphose did so at smaller size than the others, it is even better support for the model of Harris (1999, pp 283–284).

The reason for slower development was probably related to the crowding experienced by tadpoles in experimental tanks. Also, the slower growth and higher mortality suggests that the tadpoles experienced crowding. Decreased growth, as a trade-off, had been expected if the tadpoles developed faster (Merilä *et al.*, 2000*a,b*). However, as this was not the case here, crowding is the most likely explanation. Such effects of crowding on growth and development rate have been shown in several studies of tadpoles (Wilbur, 1977*b*; Dash & Hota, 1980; Semlitsch & Caldwell, 1982; Cummins, 1989; Beck, 1997; Merilä *et al.*, 2000*a*). Also, Wilbur (1987) found an effect of crowding on development in *Bufo americanus*: this led actually to the elimination of crowded tadpoles in tanks with a short hydroperiod.

In a similar experiment (with *Bufo calamita* tadpoles), Reques & Tejedo (1997) found a variation between sibships in their response. One reacted similarly to the pattern observed in this study, but most showed no response to hydroperiod, regardless of tadpole density. Also, Brady & Griffiths (2000) report a similar experiment. They found no effect of the water level treatment on time to metamorphosis in either of the three species' studied (*Rana temporaria, Bufo bufo*, and *B. calamita*). However, size at metamorphosis was smaller for tadpoles in drying tanks, and they also concluded that crowding had prevented any acceleration of development.

The experiment cannot disprove that, under some conditions, tadpoles are capable of an adaptive response to pond desiccation. Indeed, Laurila & Kujasalo (1999), Loman (1999) and Merilä *et al.* (2000*b*) have demonstrated experimentally that *R. temporaria* can increase development rate adaptively when threatened by drying. However, this study demonstrates there is a limit to this ability. It had definitely been in the crowded tadpoles' best interest to abandon the drying tanks. This is because such conditions in nature had been an indication that the pond would dry completely in the immediate future, and also because the crowding by itself reduced the available food resources. However, if crowding is sufficiently intense, the tadpoles are apparently unable to increase development rate.

The experiment by Loman (1999), that did demonstrate a plastic development rate in response to drying in

R. temporaria, was similar in set-up to the present experiment. However, there were two differences that both contributed to reduced competition in that instance. First, the experiment used 80 or 20 tadpoles per tank (rather than 80 as in the present study). Second, water was not reduced until very late, i.e. 23-26 June. This was when the earliest developing tadpoles' front legs emerged (Gosner stage 41-42; McDiarmid & Altig, 1999), and more than a month later than in the present study. There was indeed a plastic response at both tank densities, but the effect was only significant when both were combined. This comparison supports the conclusion that competition can prevent a plastic response. The comparison between the two experiments also shows that *R. temporaria* tadpoles are capable of reacting plastically even if the cue appears very late in development.

What is the situation tadpoles in drying ponds experience in nature? This depends on the shape of the pond. If the remaining water stays in one or a few small depressions (Fig. 7A), it is common for these to contain a high density of tadpoles, mimicking the experiment (Brady & Griffiths, 2000). If so, my results suggest that they may not be able to perform an "emergency" metamorphosis. The situation in the natural pond studied here conformed to this scenario and the result was similar to that in the experiment. Although no measures of densities could be made, the picture was the same in both. Under drying conditions, tadpoles were both smaller and less developed, apparently unable to escape desiccation by accelerating development rate.

On the other hand, if the original density is low or if the water depth is even, so that the area of water is independent of water depth (Fig. 7B), it is possible that tadpoles can experience drying without substantial resource reduction. Whether tadpoles of these species under such conditions do speed up development in the field remains unsettled.

So, if reduced water level leads to increased density of tadpoles, which is likely to happen in many natural situations, this results in crowding effects that oppose tendencies to increase development rate.

ACKNOWLEDGEMENTS

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