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Plastic response to pond drying in tadpoles *Rana temporaria*: tests of cost models

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ABSTRACT

Tadpoles from two types of ponds, temporary and permanent, were raised in a common garden experiment. There was no clear effect of pond type on development rate (time for metamorphosis). From each sibship, one group was raised under a constant water regime (deep tanks) and one was subject to simulated pond drying (shallow tanks). The tadpoles exhibited a plastic response to pond drying: they metamorphosed earlier in the shallow than in the deep tanks. There was no interaction between pond type and tank type; that is, there was no indication of microevolution on plasticity *per se*. Sibships with a high degree of plasticity (much earlier metamorphosis in shallow than in deep tanks) had a larger size reduction from deep to shallow tanks, suggesting a trade-off between time and size. This may be considered an allocation cost *sensu* Tollrian and Harvell (1999). However, tadpoles from early sibships that were plastic were of a similar size to those from early sibships that were not plastic (those that were early in the deep tank as well). This suggests that there was no production cost *sensu* DeWitt *et al.* (1998). Sibships with high plasticity had tadpoles that grew large in the deep tank and developed slowly (late metamorphosis) in this tank. This suggests that plastic tadpoles were those that, because of their size, most readily could afford any costs associated with plasticity and those that, because of slow development, most easily could increase development rate. The relation to size is the opposite to that predicted if the capacity for plasticity is associated with cost (plasticity cost *sensu* Tollrian and Harvell, 1999; maintenance cost *sensu* De Witt *et al.*, 1998).

Keywords: adaptation, anuran, hydroperiod, metamorphosis, microevolution, plasticity.

INTRODUCTION

The idea that plasticity is under selection rests on the assumption that plasticity *per se* is in some respect costly (Schlichting and Pigliucci, 1998), otherwise all populations should be plastic. This could mean that the ability to respond plastically is connected with fitness costs. Thus, building the physiological system necessary for a plastic response means sacrificing something else. Alternatively, the ‘cost’ may be paid only by those individuals that react plastically. Inducible defence is one example of plasticity and a cost is paid only by those individuals that exhibit such defences (physiological, developmental, behavioural).

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Such costs imply that there is an optimal trait expression in the absence of the environmental factor (predation, drying) and that alternative morphologies or development rates are suboptimal. An alternative explanation could be ‘trade-offs’. These two types of costs have been termed ‘plasticity costs’ and ‘allocation costs’, respectively, by Tollrian and Harvell (1999).

DeWitt *et al.* (1998) used a more restricted concept of cost. The second type described above relates to what they called ‘production costs’. However, to count as a production cost, performance not only needs to be lower than that for individuals not adapting to the particular environmental condition, it must also be less than that for individuals under the same conditions but possessing the same trait as a fixed inherited character. This can rarely be tested. The first type of cost described above corresponds to what DeWitt *et al.* (1998) termed ‘maintenance costs’. Scheiner and Berrigan (1998) used production costs and maintenance costs in the same way as DeWitt *et al.* (1998). They also recognized allocation costs *sensu* Tollrian and Harvell (1999) but referred to these as ‘direct costs’.

Many frogs breed in temporary ponds. This means that tadpoles must complete development before the pond vanishes. For species like the common frog *Rana temporaria*, which breeds in a wide range of ponds, from temporary to permanent (Cooke, 1985; Kutenkov and Panarin, 1995; Loman, 1996), this poses a problem. How can the frogs utilize the profitable aquatic habitat to its full potential while also avoiding desiccation when living in a temporary pond? There are two solutions: microevolution and plasticity. Microevolution means that each population can adapt to the degree of permanency of its breeding pond. There are several problems with this. Adaption may be imperfect because of gene flow and genetic drift (Falconer and Mackay, 1996; Storfer and Sih, 1998). Also, the hydroperiod of temporary ponds is usually not predictable. In dry years the ponds are of short duration, whereas in rainy years water may remain for much longer. This means that a genetically fixed strategy cannot be optimal in all years. The alternative solution is plasticity in development rate. This means that development rate varies according to the actual or perceived risk of drying – as water level (or some other cue) changes, development rate increases. This trait, plasticity, has been demonstrated experimentally for many frog species, including the common frog (Laurila and Kujasalo, 1999; Loman, 1999; Merilä *et al.*, 2000). Plasticity as a trait is also liable for selection (Scheiner, 1993; Via *et al.*, 1995; Pigliucci, 1996). If this is the case, one might expect that populations breeding in ponds with variable permanency are also more plastic than those breeding in predictable (usually permanent) ponds.

In southern Sweden, common frogs *Rana temporaria* breed in a range of habitats in terms of pond permanency. This study explored if these populations vary in development rate, either according to microevolution (i.e. selection for a fixed optimum) or plasticity. We tested the hypothesis that variation in development rate is subject to microevolution by comparing, in a common garden experiment, performance of tadpoles from populations living in natural temporary pools with tadpoles from populations in natural permanent pools. We tested the hypothesis that development rate is an adaptive, plastic character by comparing the development rate of tadpoles raised in simulated temporary ponds with that of tadpoles raised in simulated permanent ponds. These experiments provided measures of plasticity that were used to test the hypothesis that plasticity *per se* is subject to microevolution. This was done by comparing plasticity of tadpoles from populations in natural temporary ponds with that of those from natural permanent ponds. The measure of plasticity was also compared with fitness-related traits that may support the hypothesis that plasticity is associated with trade-offs or costs. To do this, we studied fitness differences between offspring families that differ in their phenotypic reactions, as suggested by Van Tienderen (1997). In particular, we tested for both 'allocation costs' (*sensu* Tollrian and Harvell, 1999) and the more restricted 'production costs' (*sensu* DeWitt *et al.* (1998). Finally, we identified traits that are characteristic of tadpoles that exhibit plasticity.

METHODS

Materials

Eggs were collected from 10 ponds in southern and central Skåne, south Sweden (Fig. 1). Five of these have repeatedly dried up (causing an estimated 50% tadpole mortality) before or during metamorphosis in the common frog over the past few years. More precisely, pond BS has dried in 6 of 7 years, DH in 6 of 7, KA in 5 of 6, SJ in 3 of 7 and SR in 5 of 7. The other five ponds have never dried enough to cause any mortality. They have all been monitored for 7 years. Most ponds are at least 1 km from each other; if closer, they are of a similar type (permanent or temporary).

From each pond, we collected egg samples from seven spawn clumps. Early laid spawn was stored at about 5°C for a few days to synchronize hatching. Thus all spawn hatched on 20 and 21 April.

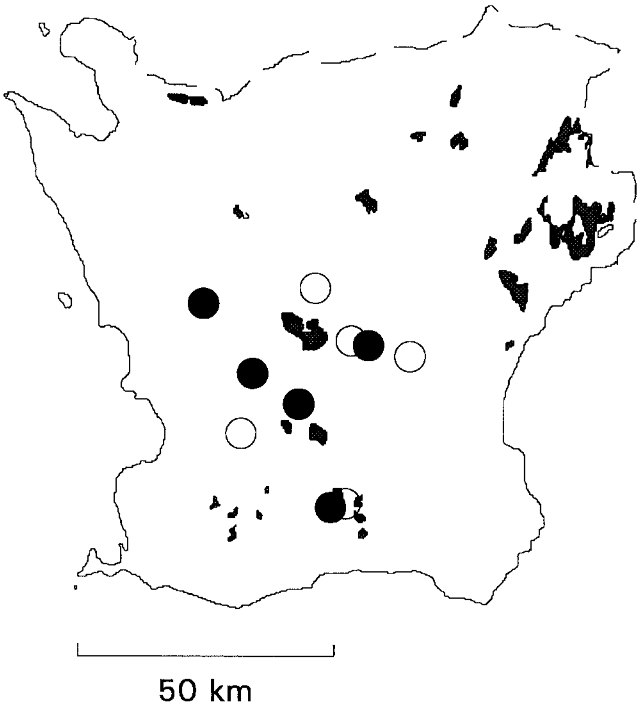

Fig. 1. Map of the study area. Solid circles are permanent ponds, open circles temporary ones.

Procedure

From each clump, 10 hatchlings each were transferred to one of two 80-litre tanks, resulting in a total of 140 tanks with 1400 tadpoles. These tanks were placed outdoors and were covered with a net for protection from predators. Algae grew on the wall of the tanks, providing food for the tadpoles. The diameter of a sample of 15 eggs from each clutch was measured. The average was used as a measure of egg size for the clutch.

On 1 June, most water was removed from one of the tanks for each pair. The depth of the remaining 5 litres of water was 2.5 cm. The depth of the other tanks remained at 25 cm.

When tadpoles approached metamorphosis, the tanks were checked daily and all tadpoles with a tail shorter than body length were removed and their body length measured (snout–urostyle). This date was recorded as the day of metamorphosis. If the tail was longer than 50% of body length, one day was added for the estimated day of metamorphosis.

Analysis

The distribution of metamorphosis dates was approximately normal, with the exception of a few very late tadpoles. The last tadpole had not metamorphosed by early December and was later lost. It lived in a deep tank. The second latest, metamorphosing on 4 September, lived in a shallow tank. As a normalizing transformation, day of metamorphosis was set to day 50 for all late outlier tadpoles (20 July).

There was some mortality; of 1400 hatchlings introduced, 1121 survived until metamorphosis. In the following analysis, only tadpoles from clutches in which at least 50% survived in the least successful of the two tanks were included. This gave 54 clutches (110 tanks) with 984 metamorphs for the analysis.

Because egg size influences day of metamorphosis (Loman, 2002b) and varies among ponds (Loman, 2001), we computed an alternative expression for development time. This was the residual in a regression of metamorphosis date on egg size. Such an analysis reveals those effects on metamorphosis date that are not modified by possible environmental and genetic effects on egg size.

For each clutch we computed the difference between the average time for metamorphosis in the deep tank and that in the corresponding shallow tank. A positive value means that the tadpoles in the shallow tank metamorphose earlier than those in the deep tank. This difference is considered a measure of average plasticity of tadpoles in the clutch.

Except when stated explicitly, all analyses are based on the average values for day of metamorphosis and metamorph size in each tank.

RESULTS

Effects of tank type and pond type on development time

There was no interaction between pond type and tank type in the effect on metamorphosis date and residual metamorphosis date (ANCOVA: $F_{1,52} = 0.50$, $P = 0.48$). However, metamorphosis date was earlier in shallow tanks ($n = 54$, mean date = 21.6 days counting from 1 June) than in deep tanks ($n = 54$, mean date = 23.1 days) (Fig. 2, Table 1). This was also true for residual metamorphosis date. In addition, there were significant effects of pond and clutch on both measures of metamorphosis date (Table 1). There were no effects of pond type.

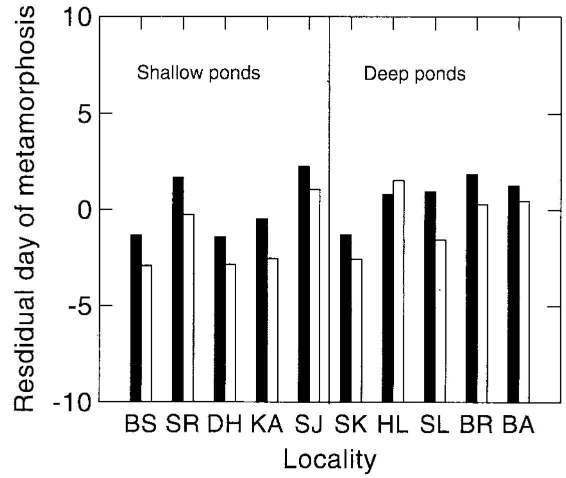

Fig. 2. Time for metamorphosis for tadpoles from the 10 ponds. Values given are the average of mean tank values. The five leftmost ponds are temporary and the five rightmost ones permanent. ■, deep tanks; □, shallow tanks.

Table 1. Results of a four-way analysis of variance for pond and tank effects on day of metamorphosis (DMM) and residual day of metamorphosis (RDMM)

		DMM		RDMM	
	d.f.	*F*	*P*	*F*	*P*
Pond type	1,8	0.47	0.51	0.78	0.40
Tank type	1,53	17.4	<0.001	17.4	<0.001
Pond	8,53	5.74	<0.001	24.8	<0.001
Clutch	45,53	7.32	<0.001	5.01	<0.001

Note: Pond type is permanent or temporary. Tank type is deep or shallow. Pond is nested under pond type. Clutch is nested under pond. The interactions between pond type and tank type were not significant (statistics are given in the text) and are not reported in this table.

Trade-off: change in development time *vs* change in size

On average, metamorphs were larger in the deep tanks (mean of tank means = 11.18 mm, $n = 54$) than in the shallow tanks (10.72 mm, $n = 54$; paired t-test: $t = 6.15$, $P < 0.001$). Furthermore, the difference in size between the deep and the shallow tanks was correlated with plasticity (difference in time for metamorphosis between the two tanks): the difference in size was greater the earlier the day of metamorphosis in the shallow tanks compared with that in the deep tanks (Fig. 3). This was assessed using a two-way analysis of covariance (ANCOVA), in which source pond was included as a correction factor (plasticity effect: $F_{1,43} = 4.97$, $P = 0.031$).

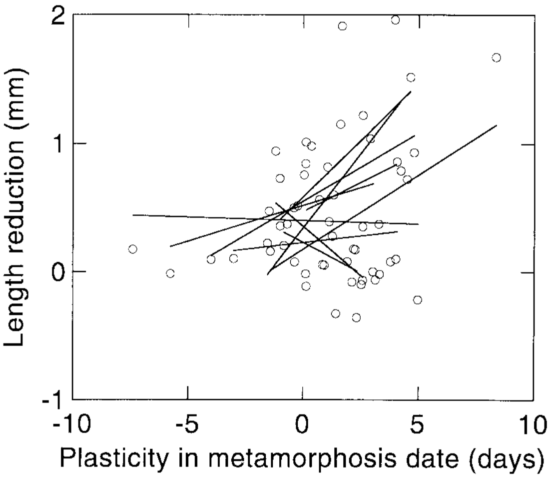

Fig. 3. Plasticity trade-offs. A high value for plasticity means that a clutch date for metamorphosis was much earlier in the shallow than in the deep tank. A high value for length reduction means that siblings raised in the shallow tank were much smaller than those in the deep tank. Each symbol represents one sibship. Within-pond linear regressions, each based on up to 7 symbols for clutches from one pond, are shown.

Correlates with plasticity

There was no correlation between egg size and plasticity ($n = 54$, Pearson's $r = -0.13$, $P = 0.34$). This was also true within source ponds (ANCOVA: $F_{1,43} = 0.52$, $P = 0.48$).

In the shallow tanks, sibships that metamorphosed early tended to be more plastic than those that metamorphosed later – that is, much of the variation in metamorphosis time was due to plasticity. This was not significant when tested using the Pearson correlation coefficient (Table 2) but was significant when pond effects were corrected for by a three-way analysis of variance (Table 2). Size at metamorphosis in the shallow tank was not related to plasticity (Table 2).

Sibships that were large at metamorphosis and/or metamorphosed later in the deep tanks tended to be more plastic than those that were smaller (Figs 4, 5). This was significant when tested with the Pearson correlation coefficient (Table 2). Both these effects were also significant within ponds when tested simultaneously with a three-way ANCOVA (Table 2).

Time for metamorphosis correlates

In deep tanks, there was no correlation between body size and time for metamorphosis (data for individual tadpoles, $n = 479$, $r = 0.066$, $P = 0.148$) (Fig. 6). In shallow tanks, however, there was a negative correlation – that is, small tadpoles metamorphosed later than large ones ($n = 483$, $r = -0.201$, $P < 0.001$). The difference between slopes was significant. This was tested with an ANCOVA, in which clutch identity was included to correct for interdependence of metamorphs from the same clutch and the difference between slopes was tested by the interaction between tank type and day of metamorphosis ($F_{1,949} = 14.39$,

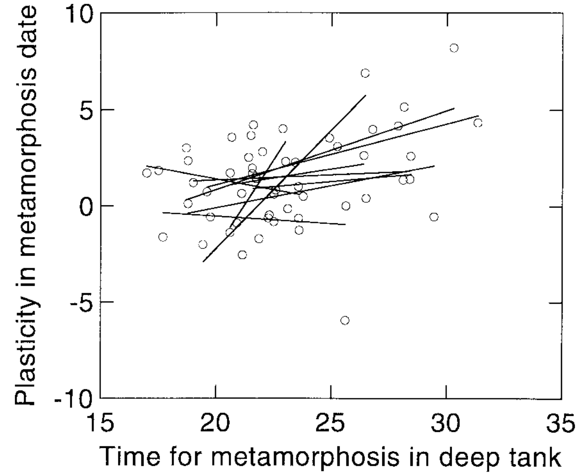

Fig. 4. Plasticity versus time for metamorphosis (deep tank). A positive value for plasticity means that a clutch date for metamorphosis was earlier in the shallow than in the deep tank. Each symbol represents one sibship. Time is given *i* number of days after 1 June. Within-pond linear regressions are shown.

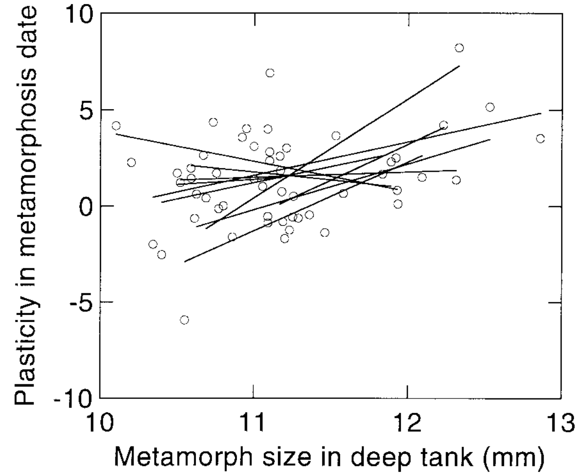

Fig. 5. Plasticity versus metamorph size (deep tank). Each symbol represents one sibship. Within-pond linear regressions are shown.

$P < 0.001$). Clutches with large eggs metamorphosed significantly earlier than those with small eggs ($n = 54$, $r = 0.47$, $P < 0.001$; Fig. 7).

Genetic and maternal effects

Although metamorphs were usually smaller in the shallow tank, there was a correlation between average body length in the deep and in the shallow tank for each clutch ($n = 54$,

Table 2. Test of factors that may affect plasticity in development rate

	ANCOVA			Correlation coefficient		
	d.f.	*F*	*P*	*n*	*r*	*P*
Deep tanks						
Source pond	9,42	1.08	0.400			
Metamorph size	1,42	7.89	0.008	54	0.32	0.057
Day of metamorphosis	1,42	6.41	0.015	54	0.34	0.034
Shallow tanks						
Source pond	9,42	0.63	0.77			
Metamorph size	1,42	0.24	0.63	54	0.13	1.00
Day of metamorphosis	1,42	4.97	0.031	54	−0.37	0.20

Note: Plasticity is the difference in days between metamorphosis in the deep and in the shallow tank for a clutch. Metamorph size and day of metamorphosis refer to the clutch's performance in the deep and shallow tank, respectively. These values are means for all tadpoles in one tank. The three leftmost columns refer to two separate (deep and shallow tanks, respectively) three-way analyses of covariance. The interactions with source pond were not significant and were removed before the final analysis. The three rightmost columns refer to four separate Pearson correlation coefficient tests. These were Bonferroni-corrected for multiple tests.

$r = 0.46$, $P < 0.001$). This was also true for time for metamorphosis in the deep and shallow tank ($n = 54$, $r = 0.75$, $P < 0.001$).

DISCUSSION

Plasticity and microevolution

Reducing the water level resulted in an earlier date of metamorphosis. The effect was on average 1.5 days, which is somewhat less than that when comparing temporary and permanent ponds in a field study in the same area (Loman, 2002c). Corresponding results have repeatedly been demonstrated in experimental studies for common frogs (Laurila and Kujasalo, 1999; Loman, 1999; Merilä *et al.*, 2000) as well as for other frogs (Tejedo and Reques, 1994; Denver *et al.*, 1998). To prove the response was adaptive, one has to show that one of the phenotypes is more fit in the environment in which it is induced. Such analyses have been performed for plant morphology in more or less crowded environments (Dudley and Schmitt, 1996) and for snail morphology in environments with different predators (DeWitt, 1996). In the present context, it means demonstrating that a fast developing tadpole is at an advantage in a drying pond. This is clear after having witnessed catastrophic mortality in temporary ponds following a dry spring (personal observation; Cooke, 1985; Loman, 1996, 2002a). Also, a late developing tadpole should be the more fit in a permanent pond. This has not been explicitly demonstrated for *R. temporaria*, but there is some evidence to support this for *R. sylvatica* (Berven and Gill, 1983). However, the assumption is usually, and in our view correctly, made when interpreting the results of studies similar to the present one (Laurila and Kujasalo, 1999; Merilä *et al.*, 2000). This point is discussed further in the final section of this discussion.

If the plasticity is sufficiently great, there is little selective pressure on time for metamorphosis *per se* as a trait (Lardner, 2000a). If so, such selection could take one of two

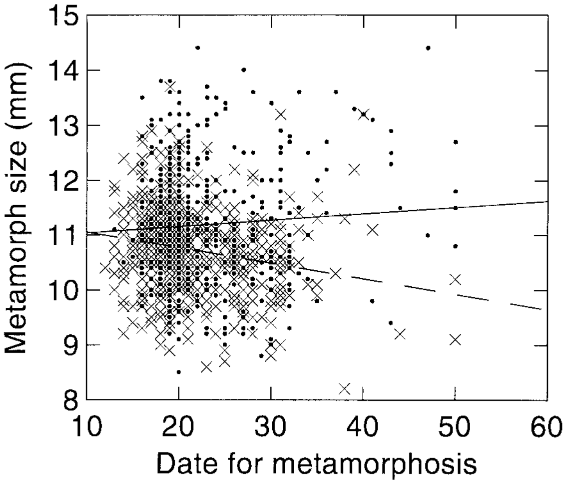

Fig. 6. Relationship between time for metamorphosis and size for individual metamorphs. The solid line is the estimated linear regression for tadpoles in the deep tanks (●) and the dashed line that for those in shallow tanks (×).

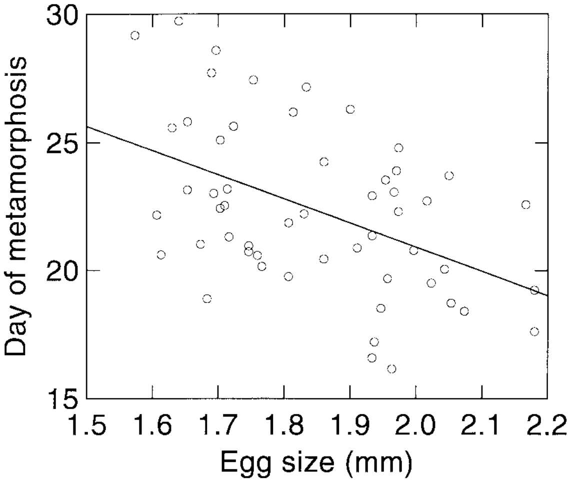

Fig. 7. Relationship between egg size and time for metamorphosis. Each symbol is one sibship. Time for metamorphosis is the mean of the values for metamorphs in deep and shallow tanks. Day is measured as the number of days after 1 June.

forms. First, the basic development rate, under a standard drying scheme (or, from the tadpole horizon, the perceived risk of drying), could be under selective pressure and differ among local populations. Given necessary assumptions of isolation, gene pool and so on (Falconer and Mackay, 1996), one could predict that tadpoles from populations breeding temporary ponds should have a higher rate of development than those from permanent ponds. Second, selection could operate on plasticity. This means that tadpoles from temporary ponds under risk of drying advance the date of metamorphosis more than tadpoles from permanent ponds under corresponding conditions.

In this study, there was no evidence for pond type effects. This does not, of course, confirm that there were none. This study was based on evolution in natural ponds. This means that there were many factors that could have contributed to the strength and direction of selection for development rate and that could not be accounted for fully, including isolation, risk of predation, competition and past history of the factors. A natural sample of ponds may have a low power to detect microevolutionary effects of hydroperiod, even if they are indeed present. Van Tienderen (1997) has explored theoretical models that suggest that genetic specialization should rarely evolve in circumstances like those studied here, where some plasticity was definitely present. Also, Reques and Tejedo (1997) noted that high genetic variation for plasticity, found by them for *Bufo calamita*, may constrain the evolution of an optimal reaction norm. There is little information from other studies on this topic. However, Newman (1988) found that spadefoot toad (*Scaphiopus couchii*) tadpoles from ponds with a short average hydroperiod developed faster, under standard conditions, than tadpoles from more permanent ponds. In the present study, selection on plasticity as a trait should have been manifest as a statistical interaction between pond type and tank type on time to metamorphosis; however, this was not the case. This corresponds to what Newman (1988) found. This poses the question: Is there a cost for plasticity?

Accelerated development: adaptive or adaptation?

Gotthard and Nylin (1995) highlighted the difficulty of separating responses that are merely beneficial for a function (adaptions) from those that are both beneficial and which evolved in direct response to the function's selection pressure (adaptations). Above, we have argued that the response was adaptive. Was the response also an adaptation? In the present context, it may be argued that shallow tanks simply were warmer and that this is the explanation for the accelerated development, as tadpoles tend to develop faster at higher temperatures (Hayes *et al.*, 1993). This, in turn, means an increased likelihood of surviving in a drying, shallow and warm pond. This is beneficial from a tadpole's point of view and the response is thus *adaptive*, but does not prove that the property is an *adaptation* to pond drying. However, there is evidence that the accelerated development represents an adaptation in the restricted sense (Gotthard and Nylin, 1995). A corresponding plasticity in development rate has been demonstrated in experiments controlling for temperature (Denver *et al.*, 1998; Merilä *et al.*, 2000). Also, in deep experimental tanks, variation between day and night temperature is less than in shallow tanks, resulting in a similar average temperature (Loman, 1999; Brady and Griffiths, 2000). This was not measured in the present study, although the set-up was similar to that in a previous study (Loman, 1999) in which temperature was measured. Also, the trade-off found means that growth rate did not increase with increasing development rate, something that would be expected if only temperature effects were involved. The present study also provides additional evidence suggesting that plasticity represents an adaptation. The experimental design meant that tanks in the shallow water treatment had higher tadpole densities and less food than tanks in the deep water treatment. By themselves, these conditions should decrease development rate (Wilbur, 1976; Murray, 1990), contrary to the actual outcome. The design was thus conservative with respect to the hypothesis that the response is an adaptation. These considerations suggest that the response was indeed an adaptation to pond drying.

Costs of plasticity

The cost of plasticity can take one of two forms. First, there may be a direct trade-off (allocation cost *sensu* Tollrian and Harvell, 1999). In the present study, this was the case in that tadpoles in shallow tanks that metamorphosed early (as a plastic response to drying) were smaller at metamorphosis than their siblings in deep tanks. A similar cost has been found when documenting a plastic response to drying (Crump, 1989; Denver *et al.*, 1998; Merilä *et al.*, 2000) and to the presence of predators (Van Buskirk and Relyea, 1998; Lardner, 2000b; Van Buskirk, 2000). In the present study, the evidence for a trade-off was even stronger, as it appeared that there was a correlation between the strength of the plastic response and the extent of the cost (reduction in size at metamorphosis) at the sibling level.

DeWitt *et al.* (1998) placed further restrictions on the concept of costs. They used the term ‘production cost’, which, in the present context, means that a tadpole that increases development rate in the face of drying pays a price, for example metamorphoses at a small size. However, this is only considered a cost if these (plastic) tadpoles are smaller (or less fit) than tadpoles metamorphosing at the same early time as part of a genetic fixed trait. In the present system, this is difficult to differentiate from the case when plasticity carries a maintenance (or plasticity) cost. Figure 8 provides an example of two costs representing different situations. In Fig. 8a, plastic individuals are always at a disadvantage compared with non-plastic individuals metamorphosing at the same time. Here, plasticity may be considered to be associated with a maintenance cost. In Fig. 8b, plastic individuals are only at a disadvantage if they metamorphose early. Because late metamorphosing, plastic tadpoles are at no disadvantage, it may be claimed that there is no maintenance cost. However, there is obviously a cost associated with metamorphosing early by means of plasticity, compared with metamorphosing early as part of a fixed strategy. In this case, it is meaningful to consider a production cost, separate from a maintenance cost. The fact that those early metamorphs in shallow tanks in our study that presumably were plastic (because there sibmates in deep tanks metamorphosed late) were of similar size (and did not metamorphose

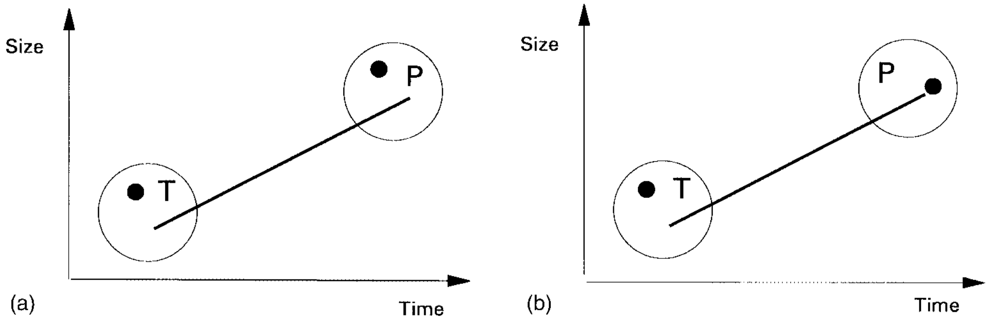

Fig. 8. Size and time for metamorphosis under two models of costs. The black dots represent phenotypes of non-plastic tadpoles. The lines represent phenotypes of plastic tadpoles. The circles indicate the response of tadpoles in two alternative environments, temporary and permanent ponds. (a) The case in which there is a maintenance cost to plasticity; the plastic tadpoles always perform worse than the locally adapted, non-plastic ones. (b) The case in which only early metamorphosing, plastic tadpoles pay a price. This is considered an example of a production cost. Both patterns (a and b) are examples of an allocation cost, as the line has a slope.

later, rather the opposite) as those early tadpoles that were less plastic (because the sibmates in deep tanks metamorphosed at a more similar date) does not support the hypothesis that plasticity in tadpoles suffers this kind of production cost.

The second type of cost is related to forming and maintaining the genetic and physiological machinery required for plasticity. This is what Tollrian and Harvell (1999) termed plasticity costs and DeWitt *et al.* (1998) termed the maintenance cost. We tried to detect such costs by comparing size in the deep tank with a sibship's degree of plasticity, expecting plastic sibships to be generally smaller and thus probably less fit under standard conditions (i.e. in the deep tank). This was not found; rather, the reverse was true. However, this test may have been rather weak, because it disregards variation in tadpole quality that is unrelated to plasticity. If there is variation in general quality among sibships, it is possible that fit sibships are larger and also more likely to bear the cost of maintaining a plasticity system. This could have masked the correlation we expected. This is discussed further below. Other studies have also failed to detect this type of cost (DeWitt, 1998; Scheiner and Berrigan, 1998). This phenomenon is modelled by Van Noordwijk and de Jong (1986) and also discussed by Lardner (2000a).

Individual variation in quality

Most discussions of costs to plasticity start by assuming that there is individual variation in plasticity, leading to variation in costs. Using a somewhat different approach, we now assume that there is individual variation in quality. If so, the present study may provide indirect evidence for costs by highlighting properties of tadpoles (actually clutches or sibling groups) that do exhibit a high degree of plasticity under standard conditions. It would appear from our results that sibships that were large in the deep tanks were more plastic than those that were small. It is reasonable to assume that size in deep tanks is a measure of high quality. Given among-pond variation in size, it may be difficult to argue that all this variation represents variation in fitness, which would imply that tadpoles in some ponds are more fit than others. However, the pattern was also present if analysed within source ponds. This variation could represent variation in fitness. Also, it is not true that these tadpoles were larger simply because of their later metamorphosis date. There was no correlation between metamorph size and time for metamorphosis in deep tanks ($n = 54$, $r = 0.10$, $P = 0.47$). The significant effect for metamorph size on plasticity was found when both time for metamorphosis and pond were controlled for (Table 2). Thus, we conclude that tadpoles that exhibited a high degree of plasticity in some respect were of higher quality than others. This may indicate that they could bear the plasticity (maintenance) cost. However, it could also (additionally or alternatively) mean that these tadpoles could bear the allocation (production) cost.

If, as we suggest, a high quality permits plasticity, one would expect sibling groups hatched from large eggs to be more plastic than others. However, this was not the case. This may be because, disregarding any effects of plasticity, tadpoles hatched from large eggs tend to develop faster than those hatched from small eggs (Berven and Chadra, 1988; Loman, 2002b; see Fig. 7). However, early metamorphosing sibling groups were less plastic than late ones, for reasons discussed below. Any direct effects of egg size on plasticity may thus have been offset by indirect effects, via development rate.

Also, sibling groups that developed slowly and thus metamorphosed late were more plastic than those that developed early. This could be interpreted in two ways. Either plasticity was less costly for these tadpoles because their basic development strategy was more ‘relaxed’, or late and early tadpoles interpreted the cue (water reduction) differently. For a late tadpole, the lowering of water on 1 June (about 4 weeks before the time for metamorphosis) was more of a threat than for an early tadpole (with a time for metamorphosis about 2.5 weeks later). This may be considered a methodological bias, but is also a picture of the real world where late developing tadpoles are more at risk when a pond approaches drying.

We observed that, at the individual level, the relationship between development rate and size at metamorphosis differed between tadpoles in deep (no or positive correlation) and shallow tanks (a negative correlation). This was also reported by Merilä *et al.* (2000). There appears to be a tendency for tadpoles to metamorphose at a fixed size or to take advantage of perceived favourable conditions in the water habitat and utilize this for growth before metamorphosis. This was the pattern for tadpoles in the deep tanks and is that predicted by the model of Wilbur and Collins (1973) for tadpoles in a predictable and favourable habitat. In this study, late tadpoles (from sibships with a slow development rate) exhibited a higher degree of plasticity than early tadpoles. This also had a price: they metamorphosed at a smaller size than early tadpoles that did not advance metamorphosis that much, as shown by the pattern for tadpoles in the shallow tanks. This pattern emerged despite the fact that these ‘plastic’ tadpoles were possibly of a higher quality. Had they been of a similar quality, they might have suffered to an even greater extent.

The experimental approach (Van Tienderen, 1997) and the discussion above rest on the assumption that there is a sibship effect on growth and development rates – that is, the rates for one individual to some extent can be predicted from those of its sibs. That there was a correlation for both traits between the deep and the shallow tanks supports this assumption.

Is reduced size really a cost?

Our results do not really prove that reduced size at an early metamorphosis represents a cost. What matters to fitness may well be the size later in the summer, when all frogs are well into their terrestrial life, or the ability to survive the first winter. Because the small, earlier metamorphs by then have spent a longer time in the terrestrial habitat, it may be that they have reached a size similar to that of the large, later metamorphs (Fig. 9). This was not within the scope of the present study and does not appear to have been considered very often in studies of developmental plasticity in the face of drying ponds. Although some field studies on amphibians have shown that large size at metamorphosis or early metamorphosis is fitness-enhancing (Smith, 1987; Semlitsch *et al.*, 1988), only one study has presented data (for *Rana sylvatica*) suggesting that metamorphosing late at a large size is better than metamorphosing early at a smaller size. The assumption that it is beneficial to remain in the aquatic habitat for as long as possible was made explicit by Wilbur (1980), although it was questioned by Werner (1986).

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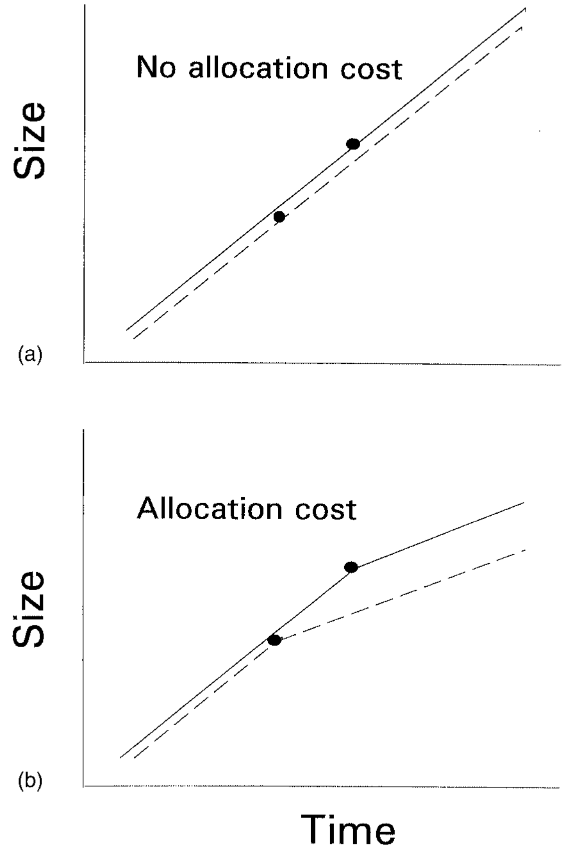

Fig. 9. Modelling tadpole and young frog growth in two contrasting environments. In (a) growth rate is similar in the terrestrial and in the aquatic habitat. In (b) growth rate decreases after metamorphosis. In (b), but not in (a), delaying metamorphosis leads to an allocation cost to fitness. Any effects of differences in predation rate are disregarded.

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