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Life history and morphology of *Rana temporaria* in response to pool permanence

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ABSTRACT

Question: How are genetic differences in life history, activity and morphology among frog populations associated with differences in pool drying rates?

Organism: The common frog, *Rana temporaria*.

Methods: Tadpoles originating from 16 different populations located on islands were reared in the laboratory at a constant water level.

Results: Activity and growth rate were positively correlated with pool drying regime and development rate was negatively correlated with the pool drying regime where tadpoles were collected. The morphology of tadpoles was also correlated with drying regime. In contrast, the weights of tadpoles were not correlated with pool drying regime.

Conclusions: The results suggest that genetic differences in life history, behaviour and morphology occur among populations and that pool drying is one of the environmental variables causing these differences.

Keywords: development, growth, life history, pool drying, *Rana temporaria*, tadpoles, temporary habitats.

INTRODUCTION

In environments where biotic and abiotic factors are relatively stable over time and space, locally adapted or specialist phenotypes are expected to evolve because selection always favours types whose fitness is highest in that environment (Futuyma and Moreno, 1988; Whitlock, 1996; Kassen and Bell, 1998). However, in spatially and temporally variable environments, selection may favour either a suite of specialized genotypes with fixed phenotypes, each adapted to a particular local environment, or flexible genotypes that express different phenotypes in different environments gaining higher fitnesses over a range of environments (Levene, 1953; Via and Lande, 1985; Futuyma and Moreno, 1988; Whitlock, 1996).

Temporary pools have become classic examples of habitats with high temporal variability, with desiccation varying between years and/or between pools (Williams, 1987; Wellborn *et al.*, 1996). Many insects and amphibians breed and spend their larval stages in small temporary pools,

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after which they metamorphose and shift habitat for the adult stages (Wellborn *et al.*, 1996). Failure to metamorphose before pond desiccation thus bears a high fitness cost (Newman, 1992). Life-history traits such as larval growth rates, metamorph size and time to metamorphosis are thus important fitness components in organisms utilizing temporary ponds, and knowledge about how these traits have evolved in response to temporally and spatially heterogeneous environments is important for understanding local adaptation.

Phenotypic plasticity has been observed in response to pond drying in a number of amphibian species. The most commonly observed response is that rates of development increase such that metamorphosis occurs earlier but at smaller sizes in the decreasing water treatments (Wilbur, 1987; Newman, 1988, 1989, 1992; Reques and Tejedo, 1997; Denver *et al.*, 1998; Laurila and Kujasalo, 1999; Merilä *et al.*, 2000; Laurila *et al.*, 2002; Loman and Claesson 2003). The observed directions of change are as predicted by models of life-history evolution in response to time constraints or disturbance regimes (Rowe and Ludwig, 1991; Lytle, 2001). The fact that plastic responses to drying rate are commonly observed and that the trait shifts would allow persistence in temporary ponds, has led most authors to conclude that the plasticity is adaptive, allowing organisms to exploit a wider range of environments than would otherwise be possible (e.g. Laurila *et al.*, 2002). However, studies of amphibians designed to investigate the interactions between evolutionary forces (e.g. selection, drift and migration) and the levels and distributions of genetic variation for plasticity have yet to provide a clear demonstration of how plasticity has evolved. For example, amphibian studies differ markedly in whether genetic variation for plasticity was detected and in its distribution within or among populations. Newman (1988), Merilä *et al.* (2000) and Laurila *et al.* (2002) observed plastic responses in the larval development traits but no within-population variation in the responses. Reques and Tejedo (1997) detected variation in plasticity within populations. Semlitsch *et al.* (1990), Laurila *et al.* (2002) and Loman and Claesson (2003) found differentiation among populations in terms of showing plastic or fixed responses, although in the study of Semlitsch *et al.* (1990), none of the differences in response were associated with the drying histories of the source ponds.

Much empirical work on the evolution of life-history traits in response to temporal variation has focused on the variation in drying rate that occurs between years (or generations). Little attention has been paid to what might be called the 'spatial heterogeneity of temporally heterogeneous habitats', for example landscapes containing mixtures of temporary and permanent pools, and the role that migration between breeding populations using pools that differ in desiccation regimes might play on the evolution of fixed or plastic phenotypes. This is somewhat surprising given that both migration, which introduces genetic variation into a population, and the frequencies of different types of environments encountered by breeding populations have been shown in theoretical models to be key parameters for predicting whether plastic or specialist types evolve in response to environmental heterogeneity (e.g. Via and Lande, 1985; Whitlock, 1996; Zhivotovsky *et al.*, 1996; Sultan and Spencer, 2002). Plasticity cannot evolve unless there is gene flow among populations that have been exposed to different environments (Via and Lande, 1985) and migration can even lower the thresholds for both environmental heterogeneity and accuracy of plastic responses above which plasticity is favoured (Sultan and Spencer, 2002). If, however, interbreeding populations encounter either one type of environment too often or too many different environments simultaneously, specialists with narrower niche widths are more likely to evolve (Whitlock, 1996).

These dynamics have led us to take a somewhat different approach to studying the potential for larval life-history traits to evolve in response to temporally variable environments. In this first of a series of investigations, we focus on sets of populations situated in

environments containing only temporary pools with low probabilities of receiving migrants from populations where larval development could occur in long-lived or permanent pools. We then ask whether patterns of larval development in these temporary pool populations provide evidence of specialization for short development times by examining associations between life-history traits scored under constant conditions and the drying rates of the pools under field conditions.

The land uplift dynamics along the Baltic coast of northern Sweden provide excellent opportunities for sampling populations with different degrees of isolation and spatial heterogeneity in pool duration. Glacial deposits, left underwater at the end of the last ice age, have gradually been raised by isostatic uplift, creating islands, which eventually merge to form mainland (Ericson and Wallentinus, 1979; Giles and Goudet, 1997) (Fig. 1). Small temporary pools are commonly formed in shallow rocky depressions on the islands. In contrast to the mainland, where temporary and permanent pools may lie in close proximity to one another, temporary pools predominate on the islands. These pools are used as the mating and larval environments of the common frog, *Rana temporaria*. We collected egg masses from temporary pools with different although rapid drying rates on 16 islands and reared the tadpoles in a common laboratory environment. We measured larval mortality, growth rates, development times, and size corresponding to the life-history traits measured in the plasticity studies cited above and predicted to change in response to environmental time constraints (Rowe and Ludwig, 1991; Lytle, 2001). In addition, we measured activity levels, since animals under severe time constraints are expected to forage more actively (Rowe and Ludwig,

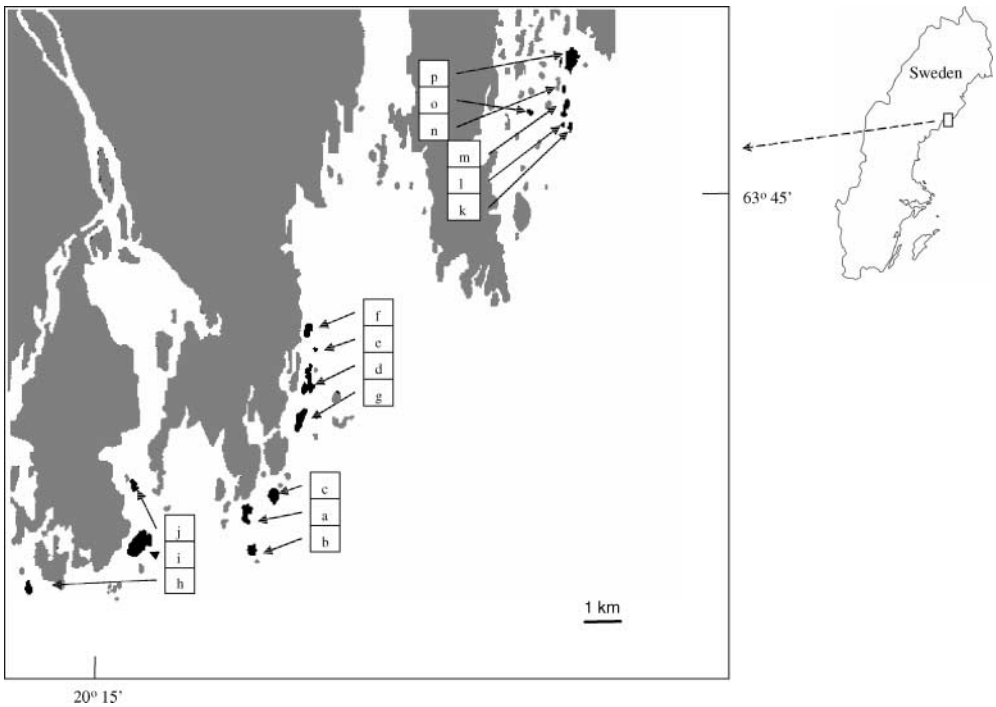

Fig. 1. Location of study populations in the archipelago of the Province of Västerbotten, central Sweden. Letters refer to populations and details of pool characteristics are given in Table 1.

1991), thus affecting growth and development (Skelly and Werner, 1990; Skelly, 1992; Johansson and Rowe, 1999), and a number of morphological traits, since changes in growth and development patterns can indirectly affect morphology through allometric relationships between body shape and size (Gould, 1977; Vermeij, 1980, 1987). We focused our analyses on the associations between the measured traits and the actual drying rate of the individual source ponds. Under a hypothesis that phenotypic specialization could occur in these populations exposed only to temporary pools, we predicted that tadpoles from pools that dry out more quickly should have higher growth rates, higher activities, faster development times and smaller sizes than tadpoles from pools that dry out more slowly.

METHODS

Study area

Rana temporaria tadpoles were sampled from 16 pools on islands in the Gulf of Bothnia east of the city of Umeå, central Sweden (Fig. 1). One pool was sampled on each island in three archipelagos south and southeast of Umeå. Pools were chosen according to the following criteria: rock pools, filled only with water from snowmelt or rain, situated at as high an altitude as possible on each island and showing signs of spawning. Some islands had more than one pool but for those islands we always chose eggs from the deepest pool. Numbers of egg batches observed in the sample pools varied between 5 and 22. These low numbers limited the number of batches we could collect without affecting the population size in the pool severely. The pools are all quite shallow and usually dry out during summer (J. Hjelm, personal observation) (Table 1). The vegetation in the pools, when present, consisted mainly of mosses (*Sphagnum* spp.), grasses and sedges and pool size varied from 1 to 17 m in maximum diameter during spring (Table 1).

Table 1. Physical characteristics of the pools studied

Population	Pool size (m^2)	Desiccation (%)	Maximum depth (2 May)
Lillhaddingen (a)	2	80	50
Petlandsskär (b)	2	100	40
Storhaddingen (c)	1.5	66	30
Lillklyvan (d)	3	66	30
Butögern (e)	1	100	40
Buten (f)	1	100	40
Ålgrundet (g)	3	100	20
Gåshällan (h)	4	100	30
Bredskär (i)	8	100	20
Österklubben (j)	2	100	40
Måsskär (k)	4	83	30
Sörtärnögern (l)	8	75	40
Nordtärnögern (m)	5	50	20
Grisselögern (n)	10	100	40
Antrevet (o)	17	66	30
Österhästskäret (p)	13	75	40

Note: Letters within parentheses denote geographic position of the population in Fig. 1.

Little is known about gene flow in *R. temporaria*, but in the closely related *R. sylvatica*, about 20% of the juveniles disperse to breed in ponds other than the one in which they hatched, although adults are 100% faithful to the pond in which they first bred (Berven and Grudzien, 1990). The *R. sylvatica* study also suggested that ponds separated by more than 1000 m should show little gene flow and a high genetic differentiation (Berven and Grudzien, 1990). These data are reasonably consistent with measurements of genetic structure of island populations of *R. temporaria* where islands are separated by distances similar to those in our study (Seppä and Laurila, 1999). This implies that gene flow among closely located islands could occur in our study site, but gene flow among islands and the mainland, where permanent as well as temporary pools occur, is less likely. Note also that the salinity of the Gulf of Bothnia is low (four parts per thousand) and unlikely to limit the migration of frogs between islands (see Seppä and Laurila, 1999).

As an effect of the last ice age, land is rising in this geographic area and it is possible to calculate the maximum age of each island (Carlsson *et al.*, 1990) and hence estimate the maximum age of the different frog populations. The ages of pools chosen in this study were estimated to range between 70 and 800 years. Given that *R. temporaria* matures at an age of 3 years in the area (Elmberg, 1991), the maximum numbers of generations for the youngest and oldest populations are 23 and 267, respectively.

Field sampling

Directly after breeding, in the middle of May 2001, egg batches from two females were collected from each pool and transported to the laboratory. At the same time we also estimated the maximum diameter and maximum depth of every pool. On 2 August, the same measurements were made, which allowed us to determine the degree of desiccation. In all analyses below we have used the pool depth measured in August divided by the pool depth in May to calculate rate of desiccation. Reduction in maximum diameter over the season gave the same qualitative pattern.

Previous studies have shown that predators have a strong impact on the life history and morphology of amphibians (Van Buskirk *et al.*, 1997; Van Buskirk and Schmidt, 2000). We sampled and estimated predator invertebrate abundance and richness in the pools in May and August. Very few predators were observed in the pools. Nine of the 16 pools had invertebrate predators with the highest density being 0.23 individuals $\cdot m^{-2}$ and the highest number of predator species was 2. Our results showed no effect of predator density on the life-history variables and morphology and we therefore do not consider the effect of predators in this study [all P-values > 0.42 in correlation analyses (F. Johansson and J. Hjelm, unpublished)].

Experimental set-up

In the laboratory, egg batches from each population and female were kept in separate containers filled with tap water. Before hatching, 10 eggs from each egg batch were measured with a digital vernier caliper, which allowed us to control for maternal effects mediated through size of eggs. When hatching occurred, we immediately chose 15 tadpoles at random from each batch. These tadpoles were divided into groups of five, and each group was placed in a small plastic container (19×15 cm; height 8.5 cm) filled with tap water to a depth of 6 cm (1.4 litres). The different populations were coded with a number and randomly placed in the experimental room to reduce the effect of *a priori* expectations and

environmental variation within the room. The day of introduction of the tadpoles was set as day 0 for the experiment. Fluorescent light tubes and natural light through windows provided light for the experiment. The artificial light gave a light : dark cycle of 18 : 6 h, corresponding to the natural light cycle. Water temperature was 20 ± 1°C during the course of the experiment. The tadpoles were fed approximately 7% of their body weight every second day with a mixture of rabbit chow and fish food. The experiment was terminated at Gosner stage 31, when the hind limbs began to be visible (Gosner, 1960).

Growth, activity, morphology and mortality

Length of the larval development was estimated as days elapsed from the start until the end of the experiment. Weight of larvae was estimated as wet weight at Gosner stage 31. To determine growth rates, the wet weight of individual tadpoles from each container was estimated to the nearest 0.001g at four different dates [days 0, 10, 19 and at Gosner stage 31 (Gosner 1960)]. A power function was fitted to the average weight at age (weight = a*age^b, r^2-values ranged between 0.96 and 0.99). The exponent b was used as a determinant of growth rate. Activity was estimated at days 5, 10, 19 and at Gosner stage 31, and defined as the proportion of tadpoles moving in each container during a 10 s observation. At Gosner stage 31, all tadpoles from each container were placed in a small glass aquarium ($35 \times 15 \times 10$ mm) in which both the lateral and ventral sides of the tadpole were photographed (28 mm macro lens) simultaneously. Morphological measurements from the photographs of tadpoles were taken with a digital vernier caliper to the nearest 0.1 mm. Morphological characters included total length, body height, body width, body length, tail height and tail muscle height (at the same place as the tail height) [for details on measurements, see Van Buskirk and McCollum (2000)].

Statistical analyses

All six containers (2 families × 3 replicates) from each locality were pooled and an average for each pool was used in all analyses. Thereafter, we examined the relationship between drying rate and activity (activity was arcsin ($\sqrt{p}$) transformed, where p is the proportion of individuals active) using linear regressions. Development time, weight and growth rate were analysed as multiple regressions of pool drying and activity including the interaction between pool drying and activity. When the interaction term was not significant it was dropped from the analyses and the data were analysed without the interaction term. An alternative approach for analysing the data set would be to use a nested design with females nested within pools and individuals within females. When we analysed our data set with a nested design the same qualitative results were achieved, but the degrees of freedom were lower due to the small number of clutches. To simplify the description of the morphological analysis, and since measurements taken are correlated, we performed a principal component analysis (PCA) on the correlation matrix to compare how overall body morphology among populations was related to pool drying and development time. Statistical significance was set at $P < 0.05$. To determine if experimental set-up (position of experimental containers) had any effect on our dependent variables – growth, development rate, activity and morphology – we divided the containers into six sections, three positioned on each side of the room. A one-way analysis of variance with section as a blocking factor showed no effect of block (all P-values > 0.49).

RESULTS

Activity and life history

Drying rate varied among pools (Table 1), and there was a positive correlation between pool drying and activity level ($r^2 = 0.42$, $F_{1,14} = 10.12$, $P = 0.007$, Fig. 2), suggesting that frogs from pools that dry out faster forage more actively.

The multiple regression on development showed that the interaction term between pool drying and activity was non-significant ($t = 0.003$, $P = 0.99$). A subsequent multiple regression without the interaction term showed that pool drying had a significant effect on development time ($t = 4.80$, $P = 0.0003$), whereas activity did not affect development time significantly ($t = 1.27$, $P = 0.22$). Hence populations that originated from pools with high rates of desiccation had faster development times (Fig. 3).

Weight at Gosner stage 31 was not affected by pool drying ($t = 1.70$, $P = 0.11$) or activity ($t = 1.82$, $P = 0.09$) and there were no significant interactions between pool drying and activity ($t = 1.71$, $P = 0.11$). These results suggest that pool drying and activity have little effect on weight at metamorphosis.

Growth rate (expressed as b) was significantly related to activity and pool drying ($t = 2.22$, $P = 0.046$ and $t = 2.19$, $P = 0.048$ respectively). In addition, the interaction term between pool drying and activity was significant ($t = 2.19$, $P = 0.049$). While activity did not influence growth rate in populations that dried completely (100%), activity increased growth rate in pools that did not dry out completely (Fig. 4). This can be seen from regression analyses where populations from pools that dried out completely were analysed separately from populations from pools that did not. For populations from pools that dried out completely, the relationship between activity and growth rate was not significant ($r^2 = 0.31$, $F_{1,6} = 2.72$, $P = 0.15$), whereas it was significant and positive for populations from pools that did not dry out completely ($r^2 = 0.66$, $F_{1,6} = 11.91$, $P = 0.014$).

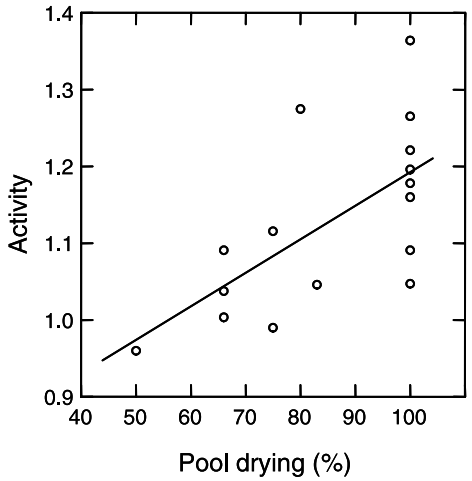

Fig. 2. Relationship between activity and pool drying for the 16 populations studied. Activity is given as arcsin ($\sqrt{p}$), where p is the proportion of individuals active. Pool drying was estimated as the reduction in water depth during the summer divided by the initial water depth. A value of 100% reflects complete drying of the pool.

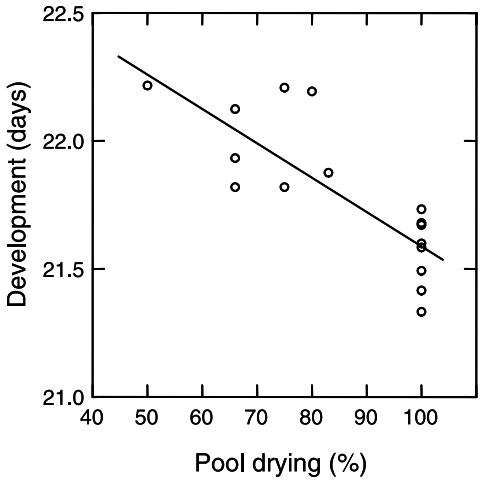

Fig. 3. Relationship between development time (number of days until Gosner stage 31) and pool drying for the 16 populations studied. Pool drying was estimated as the reduction in water depth during the summer divided by the initial water depth. A value of 100% reflects complete drying of the pool.

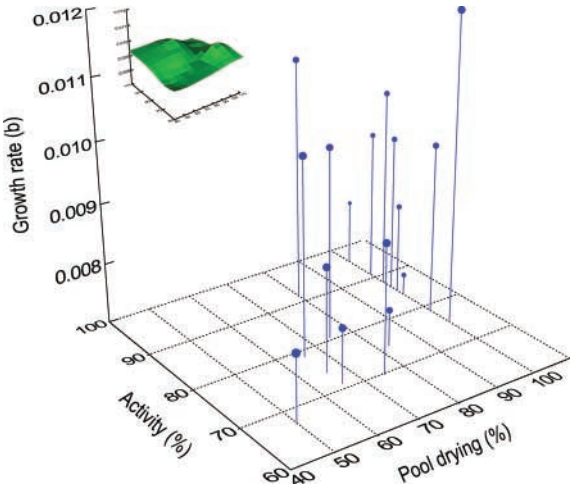

Fig. 4 Relationship between growth rate (*b*), pool drying and activity of tadpoles for the 16 populations studied. Spikes were added to data points to facilitate interpretation. The insert shows an inverse squared distance smoothing of the data points. It is added to help interpretation of the data points. The height of the curve at a smoothing point is the weighted average of the y values at x values, where the weights are the squared Euclidean distances from the data points to the smoothing point on the x axis.

A few individuals died in the containers before they reached Gosner stage 31. This mortality did not influence the development rate or growth rate of remaining individuals, since no correlations were found between either mortality and development rate or mortality and growth rate (development rate: $r^2 = 0.02$, $F_{1,14} = 0.38$, $P = 0.54$; growth rate: $r^2 = 0.09$, $F_{1,14} = 1.96$, $P = 0.17$).

Morphology

The morphology analysed with a PCA on the correlation matrix showed that the first three principal components (PCs) explained 75.8% of the variance (PC1 = 34.4%, PC2 = 25.0%, PC3 = 16.4%). PC1 was best described by body height, body length and tail height; PC2 was best described by body width and muscle height; and PC3 was best described by total length (Table 2). Overall, tadpole morphologies described by PC1 and PC3 were positively correlated to pool drying (Fig. 5) (PC1: $r^2 = 0.36$, $F_{1,14} = 7.92$, $P < 0.014$; PC3: $r^2 = 0.21$, $F_{1,14} = 3.77$, $P < 0.07$), while PC2 was not related to pool drying ($r^2 = 0.02$, $F_{1,14} = 0.28$, $P = 0.60$). Development was positively related to PC1 ($r^2 = 0.38$, $F_{1,14} = 8.65$, $P = 0.011$), but no significant correlations with PC2 or PC3 were detected (PC2: $r^2 = 0.001$, $F_{1,14} = 0.017$, $P = 0.89$; PC3: $r^2 = 0.05$, $F_{1,14} = 0.82$, $P = 0.38$).

Table 2. Factor loadings of the morphological variables of tadpoles from the principal component analysis

	PC1	PC2	PC3
Total length	0.53	−0.22	0.77
Body height	0.67	0.20	−0.54
Body width	0.04	0.81	0.12
Body length	−0.63	−0.44	0.01
Tail height	−0.90	0.11	−0.05
Muscle height	−0.32	0.73	0.25

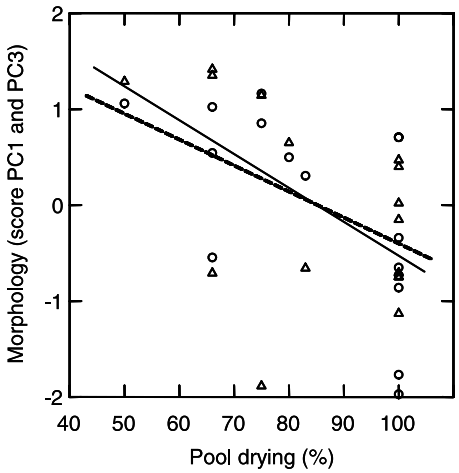

Fig. 5. Relationship between morphology (scores from PC1 and PC3) and pool drying for the 16 populations studied. Pool drying was estimated as the reduction in water depth during the summer divided by the initial water depth. A value of 100% reflects complete drying of the pool. Dots and the solid line denote PC1, while triangles and the dashed line denote PC3.

Maternal effects

Egg size could be influenced by genetic and/or maternal effects. To determine the extent to which maternal effects (egg size) affected life-history and morphological characters, we constructed correlation matrices between average egg size and degree of desiccation, activity, growth rate (*b*), time to Gosner stage 31, mortality, PC1, PC2 and PC3. Egg size was only correlated significantly (two-tailed) to PC1 describing morphology (Spearman correlation $r = -0.44$, $P = 0.042$). In a similar analysis where we constructed correlation matrices between the coefficient of variation in egg size and the degree of desiccation, coefficient of variation in activity, growth rate (*b*), time to Gosner stage 31, mortality, PC1, PC2 and PC3, we found a similar pattern that the coefficient of variation of PC1 was weakly correlated to egg size (Spearman correlation $r = -0.47$, $P = 0.03$). This result suggests that PC1, a combined morphological trait, may be affected maternally.

DISCUSSION

Rana temporaria, like many other frog species, breeds in a wide variety of ponds from temporary to permanent (Loman, 2002; Loman and Claesson, 2003). The minimum criterion for an individual to make a contribution to the next generation is that larval development must be completed before pool drying occurs. Laboratory studies have shown that tadpoles of several species, including *R. temporaria*, can increase their rates of development as a phenotypically plastic response to decreasing water levels (Denver *et al.*, 1998; Laurila and Kujasalo, 1999; Laurila *et al.*, 2002). However, theory suggests that if migration rates are low, or gene exchange occurs among populations exposed to similar types of drying regimes, phenotypic specialization rather than plasticity may be more likely (Via and Lande, 1985; Whitlock, 1996; Zhivotovsky *et al.*, 1996; Sultan and Spencer, 2002). The main purpose of our study was to explore to what extent *R. temporaria* tadpoles from isolated environments containing only temporary pools, although with varying drying rates, differed in life history. Under these conditions, we expect to find positive associations of life-history traits with drying rate, and we observed that frogs sampled from pools that dried faster had faster development and higher growth rates when raised under conditions simulating permanent water availability. Although size and time to metamorphosis have significant heritabilities in frogs (Berven and Gill, 1983; Travis *et al.*, 1987; Newman, 1988; Semlitsch, 1993; Laurila *et al.*, 2002), previous studies that looked for correlations between life-history traits and pool drying among populations only found weak evidence for such correlations (Semlitsch *et al.*, 1990; Reques and Tejedo, 1997; Loman and Claesson, 2003). Hence, our study is one of the first to suggest this pattern.

One reason why we found a strong association between life-history traits and pool drying when other studies did not might be that our populations are influenced to a lesser extent by gene flow. Assuming that *R. temporaria* has dispersal probabilities similar to *R. sylvatica* (Berven and Grudzien, 1990), about 20% of the juveniles metamorphosing from temporary pools on an island may disperse to other pools within neighbourhoods of about 1000 m radius. Most of the islands within our archipelagos are separated by just over 1 km (Fig. 1) and, more importantly, any gene exchange that does occur between pools within or among islands is most likely to involve individuals that have completed metamorphosis in temporary pools. In addition, those *R. temporaria* adults that breed in their original pools have been selected to a drying rate specific to those temporary pools. This will further strengthen the probability of phenotypic specialization.

Since we found no relationship between activity and growth rate in populations where pools dried out completely, we suggest that the higher growth rates of populations from pools that dried out faster were mediated independent of activity. Instead, we interpret the high growth rate in larvae from pools that dried out quickly as an effect of a higher intrinsic growth rate mediated by a physiological process, for example digestion efficiency. Such growth rate responses mediated by physiological processes independent of activity components have been found in insects (Johansson and Rowe, 1999) and among tadpoles of different frog species (Richardson, 2001). In contrast, we found a significant relationship between activity and growth rates in pools that did not dry out completely. Tadpoles from pools that always dry out at a fast rate need to develop quickly and the ability to adjust growth rate in terms of activity might be of minor importance. However, growing at a fast rate might be costly (Arendt, 1997) and therefore such costs could be reduced by adjustments in foraging activity. Tadpoles from populations that do not dry out completely seem to reduce such costs and instead adjust growth rate with activity, as suggested by the positive associations observed between growth rate and activity in this study. Costs of activity are also plausible but such costs are mainly associated with predation risk (Werner and Anholt, 1993) and predator densities did not differ between populations.

Despite the fact that growth rate and development showed a positive correlation with pool drying, no correlations between size (weight) and pool drying were found. Since size is an important component of fitness in frogs (see Laurila *et al.*, 2002; Altwegg and Reyer, 2003 and references therein), we suggest that the absence of a pool drying effect on size is due to a need for a minimum size at metamorphosis, given that larvae below this size have low, first-winter survival probabilities (Altwegg and Reyer, 2003). We suggest that the higher growth rate and faster development of populations from pools that dried out faster cancelled out and resulted in no difference in size among populations. Newman (1988) also found no differences in size at metamorphosis among five populations of spadefoot toads but his study was based on one sibship only from each population. In contrast, Laurila *et al.* (2002) found differences in size at metamorphosis among distantly separated populations. The present study and that of Newman (1988) cover smaller geographic distances among pools where climatic conditions affecting body size should be of minor importance compared with the study by Laurila *et al.* (2002), where the two study pools were separated by 1400 m.

Morphology was related to drying rate, but currently we have no single explanation for the relationship between pool drying and morphology. It could be due to allometric growth and development effects. Animals developing or growing at different rates might end up with different morphologies because overall growth or development might not have the same effect on all body parts (see references in Forsman, 1996). Under the assumption that populations were founded by few individuals, the observed morphological differences could also be due to founder effects. In this case, the relationships between the life-history variables and morphology represent spurious effects. The observed differences in life history and morphology might also arise from differences in microclimatic conditions between pools rather than pool drying rates *per se*. Local climatic factors such as temperature have been suggested to affect life-history traits in *R. temporaria* (Ståhlberg *et al.*, 2001), which could in turn affect morphology, but since the greatest distance between two islands is 20 km we find this effect unlikely. Finally, anuran larvae have been shown to differ in morphology among populations in response to predators (Van Buskirk and Schmidt, 2000). A predator effect seems unlikely in our study, since few predators were present in these pools and no relationships between predator densities and morphology or life history were found.

The probability that non-genetic maternal effects led to the observed differences among populations in morphology cannot be ruled out completely. In general, maternal effects in *R. temporaria* on life-history traits are not strong (Merilä *et al.*, 2000; Laurila *et al.*, 2002), and when present have been mediated through egg size (Laugen *et al.*, 2002). Egg size was positively correlated with morphology (PC1). Egg size was not, however, correlated with any of the life-history characters or activity. We would also stress that life-history traits in anurans are usually affected by a combination of genetic and maternal effects (Travis, 1981; Berven, 1982; Merilä *et al.*, 2000). Therefore, we find it unlikely that our result is only due to maternal effects. Even if maternal effects are present, they could be genetic as a result of differences in maternal investment caused by adaptations to different environments (Mousseau and Fox, 1998).

Admittedly, we did not study plasticity or genetic variation in the traits we focused on. Such information would be valuable in supporting the hypothesis that natural selection has caused the observed differences in life history between the populations. Some of the larger islands and the mainland surrounding the archipelagos consist of mosaics of temporary and permanent pools. In such areas, we expect a larger genetic variation and a greater plasticity since individuals are living in more heterogeneous environments. In contrast, populations on small islands with only one pond type should show less variation given low gene flow between heterogeneous environments. As revealed by the review in the Introduction, studies on plasticity and genetic variation show that both within- and among-population genetic variation occur as an effect of pool origin, but so far no clear evidence exists that drying rate has caused these patterns. We are currently investigating genetic variation in our populations since this might reveal patterns of adaptations to pool drying.

In summary, we found that development rate, growth rate, activity and morphology were related to the drying rate of pools. We propose that the effect of pool drying on life-history characters shown in this study is associated with low gene flow among islands whose pools, although somewhat variable in drying rate, are all temporary. If we consider the temporary pools as predictable environments, the observed differences among populations might be a result of stabilizing or directional selection acting on the these traits. Accepting that the observed differences between populations are due to selective forces or founder effects, the evolution of life histories and morphology has occurred within less than 267 generations, which is a short time span. Populations can, however, be younger than this, since we do not know when islands were colonized. Micro-evolutionary changes in life history have been shown to occur within fewer generations than in our study system (Reznick *et al.*, 1997), and hence it is likely that natural selection has caused the differences among populations.

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