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Heads or tails? Variation in tadpole body proportions in response to temperature and food stress

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ABSTRACT

Given sufficient time and genetic variation, populations of ectothermic animals living in different thermal environments are expected to diverge in their thermal optima for growth. Several recent studies have used common frog (*Rana temporaria*) tadpoles as models to study animal adaptation to geographic variation in ambient temperatures, but little attention has been paid to how the growth of different body parts responds to variation in temperature. We examined the variation in early growth in body, tail and relative tail length of common frog tadpoles in a common garden experiment that subjected individuals from six populations situated along a 1600-km latitudinal gradient to different temperature and food treatments. We found a high degree of latitudinally unordered inter-populational differentiation in relative tail length, and that increasing levels of environmental stress (low temperature and restricted food) lead to increased mean relative tail length. This occurred mainly because of changes in body growth, not because of changes in tail growth *per se*. This suggests that growth of the tail itself is less sensitive to environmental stress than body growth, but at the same time the relative length of tail can be a good indicator of growth conditions experienced by individuals. In general, the results do not support the earlier proposition that common frog tadpoles in the south have relatively longer tails due to increased risk of predation, but indirect evidence was found to support the contention that the populations along the latitudinal gradient have different thermal optima for growth as indicated by latitudinally ordered differences in how relative tail length changed in response to temperature treatments.

Keywords: adaptation, growth, latitude, *Rana temporaria*, tail length, thermal optima.

INTRODUCTION

Growth rate is an important life-history trait, and a lot of theoretical and empirical work has been done to understand both ultimate and proximate determinants of growth rate variation in the wild (Roff, 1992, 2002; Stearns, 1992; Arendt, 1997). Due to the ease with which tadpoles can be reared and manipulated in controlled large-scale experiments,

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amphibian models have had a central role in testing and developing life-history models of growth and development (e.g. Wilbur and Collins, 1973; Berven *et al.*, 1979; Berven and Gill, 1983; Alford and Harris, 1988; Rowe and Ludwig, 1991; Day and Rowe 2002). Since tadpole growth rates are strongly affected by both abiotic and biotic factors (reviewed in Alford, 1999), amphibians have also been popular models for studies in physiological ecology (Feder and Burggren, 1992). Furthermore, in the realm of evolutionary ecology, tadpole anti-predator defences and their relationship to growth have received considerable attention (e.g. McCollum and Van Buskirk, 1996; Anholt and Werner, 1999; Van Buskirk, 2000).

Recently, amphibian adaptation to latitudinal and altitudinal variation in thermal environment has gained a renewed interest (Martin and Miaud, 1999; Merilä *et al.*, 2000a; Laurila *et al.*, 2001; Ståhlberg *et al.*, 2001; Laugen *et al.*, 2002, 2003a,b; Olsson and Uller, 2002; Pahkala *et al.*, 2002). As in studies of other ectotherms (e.g. Levinton, 1983; Levinton and Monahan, 1983; Lonsdale and Levinton, 1985; Dittman, 1997), there is evidence to support the contention that populations are locally adapted to the temperature they most commonly encounter in their natural environment (Ståhlberg *et al.*, 2001; Laugen *et al.*, 2003a). Furthermore, based on the reasonable assumption that the risk of predation is higher for the southern than for the northern Scandinavian common frog tadpoles (*Rana temporaria*), Ståhlberg *et al.* (2001) interpreted the longer relative tail length of southern tadpoles to be an adaptation to life under predation risk. In addition, since northern tadpoles seem to experience higher water temperatures than the southern tadpoles during their development (Ståhlberg *et al.*, 2001; Cummins, 2003), they further inferred that the relatively long tails of northern tadpoles in high temperatures (20°C), and the relatively long tails of southern tadpoles in low temperatures (10 and 15°C), would support the adaptive hypothesis that the tadpoles grow longer tails at the temperatures which 'they normally have to evade predators' (Ståhlberg *et al.*, 2001).

Although the results and inference of Ståhlberg *et al.* (2001) are intriguing, they are open to alternative interpretations. First, variation in relative tail length is not considered to be an important anti-predator trait in common frog tadpoles, but deeper tail fins and tail muscles are induced as a morphological response to predation risk in this species (Lardner, 2000; Van Buskirk, 2001). In fact, the existing literature gives little reason to believe that tail length *per se* is in any way related to tadpoles' ability to avoid predation (but see Kaplan, 1992; Teplitsky *et al.*, 2003). Therefore, an alternative explanation is that variation in relative tail length between populations – as assessed in a common garden situation – reflects variation that has evolved in response to some other, yet unidentified demand. It is also possible that variation in relative tail length has nothing to do with adaptation to particular environmental conditions *per se*, but reflects merely a correlated (allometric) response to selection on some other trait(s). The fact that the relative tail length of tadpoles seems to be sensitive to temperature variation during development (Kaplan, 1992; Ståhlberg *et al.*, 2001) hints at the possibility that variation in tail length could be indicative of the degree of environmental stress experienced by tadpoles. Because of trade-offs in allocation of resources to different functions and traits, growth in different body parts or traits under different environmental conditions may differ depending on their functional importance according to evolved allocation rules. For instance, when faced with suboptimal feeding conditions or temperatures, tadpoles might give priority to body growth at the cost of tail growth. Under this hypothesis, we should expect to see relatively short tails under growth-limiting conditions. In other words, absolute tail length could be insensitive to the effects of stress, and differences in relative tail length could be caused by sensitivity of body growth to environmental stress. Second, as the study of Stålhberg *et al.* (2001) was based on data collected from one 'southern' (58°N) and one 'northern' (65°N) Swedish population of common frogs, the results do not allow rigorous deduction and generalization to infer whether variation in tail length actually shows any latitudinal patterns.

In this study, our aims were (1) to determine whether there is a general latitudinal trend for shorter tailed common frog tadpoles towards the north across Scandinavia, and (2) to establish whether low temperature in general induces longer tails in southern Scandinavian common frogs, but shorter tails in northern Scandinavian common frogs. To do this, we analysed data from six common frog populations collected along a 1600-km latitudinal cline spanning four degrees of latitude (i.e. ~440 km) further south and north than the data presented in Stålhberg *et al.* (2001). As the tadpoles from all these populations were also subjected to common garden experiments under three temperature and two food treatments, we were able to evaluate also how multiple stress influenced the development of relative tail length, and whether these effects were consistent across different populations.

METHODS

Basic information about the study species and populations (Lund: 55°40′N, 13°27′E; Uppsala 59°40′N, 17°15′E; Umeå 63°50′N, 20°25′E; Ammarnäs 65°54′N, 16°18′E; Kiruna 67°52′, 20°29′; Kilpisjärvi 69°04′N, 20°50′E) are given in Laugen *et al.* (2003b) and Palo *et al.* (2003), where also the methods for obtaining samples and general rearing conditions and procedures are described in detail. In brief, all larvae used in the experiments were obtained from laboratory crosses of adults collected from spawning sites at the onset of the breeding season, except for the Ammarnäs population, for which eight freshly laid spawn clumps were collected from the wild (see below). These procedures ensured that all tadpoles were of the same age at the start of the experiment and, apart from the Ammarnäs population, subject to the same early life environmental effects, such as acclimatization to field temperatures (e.g. Hoffmann *et al.*, 2003). In all but the Umeå and Ammarnäs (see above) populations, 16 maternal half-sib families (i.e. 32 full-sib families) were created where eggs from each of eight females were fertilized by sperm from two of 16 males. The Umeå tadpoles stem from 32 maternal half-sib families (16 females and 32 males used). Due to the large difference in the onset of spawning among the populations (Merilä *et al.*, 2000b), the starting dates for the experiments also differed. In the case of the southernmost population (Lund), the fertilizations were performed on 9 April 1998, whereas in the case of the northernmost population (Kilpisjärvi), the corresponding date was 4 June 1998. However, the rearing conditions were identical for all populations (see below).

The crossings were carried out as explained in Laugen *et al.* (2002). Following fertilization, eggs were divided into three different temperature treatments (14 ± 1°C, 18 ± 1°C and 22 ± 1°C; two bowls per cross in each temperature), where they were kept until hatching. Water was changed every third day during embryonic development. When most of the embryos in a given temperature treatment had reached Gosner stage 25 (Gosner, 1960), eight randomly chosen tadpoles from each cross were placed individually (to avoid confounding density/competition effects in face of mortality) in 0.9-litre opaque plastic containers in each of two food treatments (restricted and *ad libitum*). This procedure was repeated for each population in the three temperature treatments resulting in 48 experimental tadpoles per cross. However, due to mortality during the experiment, the final number of tadpoles per family was typically less than this. Every seventh day the tadpoles were fed a finely ground 1 : 3 mixture of fish flakes (TetraMin, Ulrich Baensch GmbH, Germany) and rodent pellets (AB Joh. Hansson, Uppsala, Sweden). The amount of food given to each tadpole was 15 mg (restricted) and 45 mg (*ad libitum*) for the first week, 30 and 90 mg for the second week, and 60 and 180 mg per week thereafter. The *ad libitum* treatment was selected to be such that the individuals did not consume all the food before the next feeding event in any of the temperature treatments. In the restricted food treatment, the tadpoles in the two highest temperature treatments consumed all of their food resources before the next feeding, indicating food limitation, but in the low temperature treatment tadpoles frequently had food left even after 7 days of feeding. Tadpoles were raised in dechlorinated tap water aerated and aged for at least 24 h before use. The water was changed every seventh day in conjunction with feeding and the photoperiod was maintained at 16 : 8 light : dark.

Twenty-one days after the experiments began, body and tail length were measured for about half of the tadpoles (a total of 2674 individuals) from each population. These measurements were made using a stereo-microscope to the nearest 0.01 mm. The reason for measuring only half of the animals was simply a logistic one. For each individual, we measured body length from the tip of nose to the base of tail, and total length from the tip of the nose to tip of the tail. Tail length was obtained by subtracting body length from total length.

To analyse population and treatment influences on growth of different body parts, we first averaged all measurements of offspring to a particular male reared in a given block (and treatment combination) mated to different females to reduce interdependence in the data. After this, we fitted a fixed effect model where the response variable (i.e. body length, tail length or relative tail length [defined as the residuals from the regression of tail length on body length]) was modelled using temperature and food treatments, population origin and block (nested within temperature treatment) as factors. The model also included all interactions between treatment effects and population origin. All reported values are least square means (± standard error) from those models.

RESULTS

With the exception of block, all effects in the model, including the interactions, explained significant amounts of variation in relative tail length (Table 1). The same was true in the case of absolute tail and body length (Table 1). Although the interpretation of the main effects is difficult in the presence of significant interaction terms, some general trends are apparent (Fig. 1). First, differences in mean relative tail length among populations were large, but these differences were not latitudinally ordered (Fig. 1a). Mean relative tail length was largest in mid-latitude populations (Uppsala and Umeå), intermediate in the three northernmost populations, and shortest in the southernmost population (Lund; Fig. 1a). This pattern followed closely that of absolute tail length (Fig. 1d), whereas body length increased until Umeå, and remained rather similar across the rest of the populations (Fig. 1h).

High temperature had a negative effect on relative tail length: tadpoles grown at 22°C developed significantly shorter tails than those grown at 14 and 18°C, but there was no significant difference between the two latter treatments (Fig. 1b). Inspection of mean absolute body and tail length changes in response to temperature treatments revealed

Table 1. Results of fixed effects analyses of variance of relative tail length, tail and body length

Source	d.f.	Relative tail length			Tail length			Body length		
		SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Block	9	105.36	1.25	0.259	212.99	2.14	0.024	635.19	9.09	<0.001
Population	5	7538.36	161.21	<0.001	10936.87	197.84	<0.001	2250.04	57.95	<0.001
Temperature	2	465.91	24.90	<0.001	61.21	2.77	0.063	578.84	37.27	<0.001
Population × temperature	10	1624.75	17.37	<0.001	1679.41	15.19	<0.001	330.21	4.25	<0.001
Food	1	250.37	26.77	<0.001	1595.45	144.30	<0.001	7698.60	991.42	<0.001
Population × food	5	113.65	2.43	0.033	479.36	8.67	<0.001	853.73	21.98	<0.001
Temperature × food	2	51.08	2.73	0.065	503.96	22.79	<0.001	1511.76	97.34	<0.001
Population × temperature × food	10	197.73	2.11	0.021	306.15	2.77	0.002	533.12	6.86	<0.001
Error	996	9314.70			11012.21			7734.15		
Model	44	10673.47	25.93	<0.001	16916.35	34.77	<0.001	14049.56	41.12	<0.001

Note: The term block was nested within temperature treatment. SS = sums of squares.

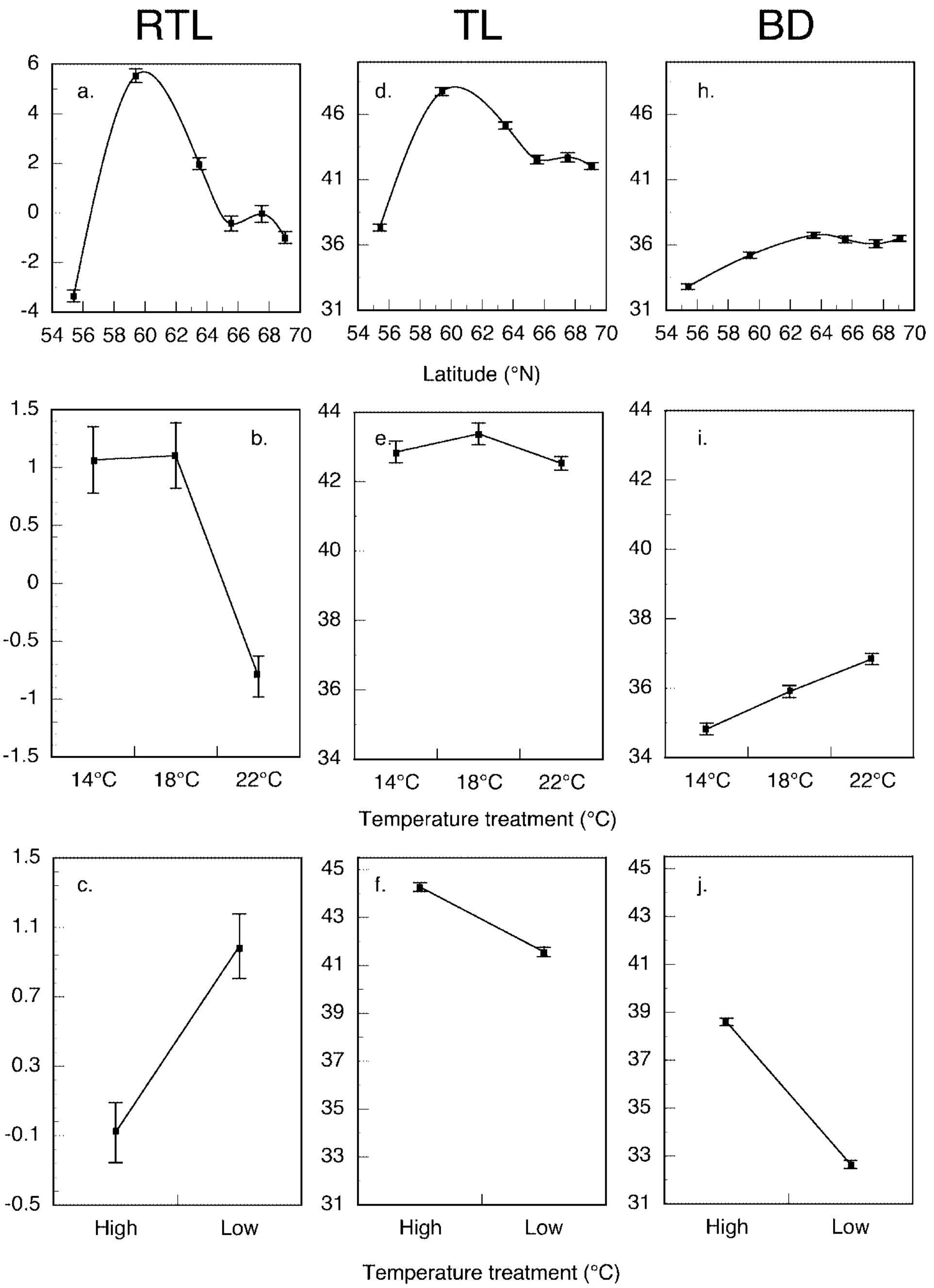

Fig. 1. Mean relative tail length (RTL), tail (TL) and body (BD) length of common frog tadpoles at age 21 days as a function of (a, d, h) population of origin, (b, e, i) temperature treatment and (c, f, j) food treatment. All values are least square means (± standard error) from the models presented in Table 1.

that while body length increased as a linear function of temperature (Fig. 1i), tail length responded much less than body length (Fig. 1e). Hence, most of the response in relative tail length was due to changes in body growth and not in tail length *per se*.

The low food condition resulted in significantly higher mean relative tail length than in the high food condition (Fig. 1c). Again, this reduction was due mainly to reduced body growth in the low food condition, rather than to changes in tail length *per se*: the reduction in body length (Fig. 1j) in response to low food was much more pronounced than the reduction in tail length (Fig. 1f).

These general trends described by the main effects hide considerable complexity in the responses as evidenced by significant interactions between all the factors (Table 1). A significant population × temperature interaction revealed that while relative tail length was rather insensitive to temperature treatments in some populations (e.g. Umeå; Fig. 2), it was a negative function of temperature in some of the populations (e.g. Ammarnäs, Uppsala) but a positive function in others (e.g. Lund; Fig. 2). Hence, no generalizations about the sensitivity of tail length development with respect to latitude are possible. The significant population × food interaction revealed that while the restricted food treatment in most populations increased relative tail length, this was not the case in the two northernmost populations (Fig. 2). An almost significant temperature × food interaction indicated that while restricted food generally increased relative tail length, this increase tended to be higher in the highest than in the two lowest temperature treatments (Fig. 2). Again, the reason for the larger response in the 22°C treatment seems to be due to a stronger response in body length than in absolute tail length (Fig. 3). Note also that low food in combination with a

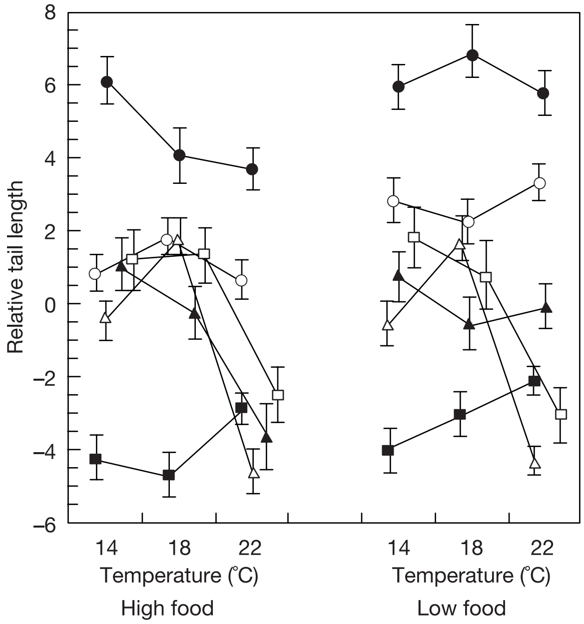

Fig. 2. Mean relative tail length in different common frog populations at age 21 days as a function of temperature and food treatments. All values are least square means (± standard error) from the model presented in Table 1. ■, Lund; ●, Uppsala; ○, Umeå; ▲, Ammarnäs; □, Kiruna; △, Kilpisjärvi.

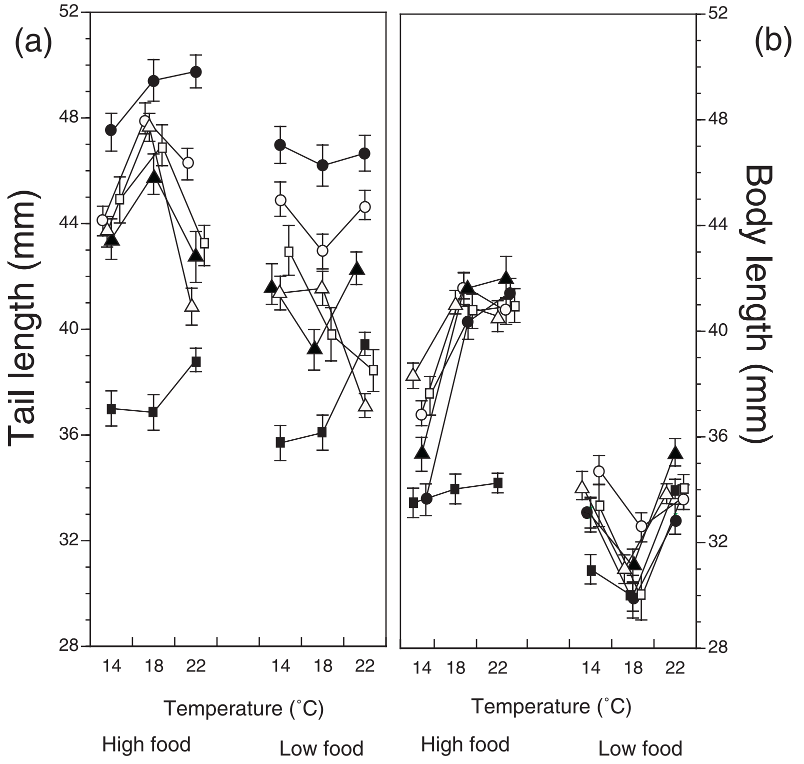

Fig. 3. Mean absolute (a) body and (b) tail length of common frog tadpoles at age 21 days as a function of temperature and food treatments. All values are least square means (± standard error) from the models presented in Table 1. ■, Lund; ●, Uppsala; ○, Umeå; ▲, Ammarnäs; □, Kiruna; △, Kilpisjärvi.

temperature of 18°C had the largest negative effect on both body length and tail length in all populations, but as these effects were largely parallel, their impact on relative tail length was small (Fig. 3). All in all, responses to different treatments were often population specific, as also indicated by significant three-way interactions between population, food and temperature in all three traits (Figs. 2 and 3).

Under the hypotheses that northern larvae are adapted to growth in higher temperatures than the southern larvae (cf. Ståhlberg *et al.*, 2001), and that variation in relative tail length is indicative of the degree of stress experienced by larvae, there should be a positive correlation between latitude and the temperature at which relative tail length in the given population is lowest. We tested this by scoring (from Fig. 2) the temperature (by food level treatment) at which relative tail length was shortest in each of the populations (if relative tail length was similar – standard errors overlapping – at two temperatures, we used the mean of these temperatures). In both food treatments, there was a positive correlation between the latitude of origin and temperature at which relative tail length was shortest (unrestricted food: $r_s = 0.88$, $n = 6$, $P = 0.021$; restricted food: $r_s = 0.97$, $n = 6$, $P = 0.001$).

DISCUSSION

Our results revealed large variation in relative tail length in response to temperature and food treatments, much of which was highly population specific. Interestingly, the main proximate explanation for this variation turned out not to be differential responses in tail length *per se*, but responses in body length. In other words, a reduction in relative tail length in response to high temperature was mainly due to relatively fast growth of the body, not reduced tail growth. Increased growth of the body is most likely to be of a positive fitness value, as all the vital organs are situated in this part of the tadpole, whereas the tail becomes completely absorbed during metamorphosis (Viertel and Richter, 1999). Indeed, body length at metamorphosis has been shown to be linked to later life fitness in several amphibians (e.g. Berven, 1990; Altwegg and Reyer, 2003). Likewise, a general increase in relative tail length in response to restricted food was mainly accounted for by a reduction in body growth. Hence, these results suggest that, within a given population, a high relative tail length is indicative of individuals' poor growth performance and vice versa. This was further supported by the finding that there was a positive correlation between latitude and the temperature at which relative tail length in a given population was lowest. This is exactly what is to be expected under the hypothesis that northern larvae are adapted to growth under higher temperatures than the southern larvae (cf. Ståhlberg *et al.*, 2001). If a relatively long tail is an indicator of poor growth conditions, southern larvae should have relatively long tails in warm conditions and northern larvae in cold conditions.

Another interesting feature of our results was the marked differentiation in the mean relative tail length among populations. In contrast to the suggestion that variation in relative tail length in this species would be latitudinally ordered (Ståhlberg *et al.*, 2001), we found little evidence for this: the highest mean relative tail length was found in the second southernmost population, and the lowest in the southernmost population. Hence, there seems to be no clear latitudinally ordered pattern in variation of relative tail length of common frog tadpoles in Scandinavia. However, although our study was based on six rather than two populations (cf. Ståhlberg *et al.*, 2001), even this may not be enough to pick up the signal of latitudinally ordered variation even if it does exist. If relative tail length is mainly an indicator of an individual's growth performance, and populations are at least to some extent adapted to specific conditions prevailing in a given locality (e.g. temperature, predation, competition), we should perhaps not even expect to see any strong latitudinal patterns in relative tail length differentiation. It is also possible that the population differences seen in common garden experiments merely reflect some maladaptation to laboratory conditions. According to this reasoning, our laboratory conditions would have been particularly unsuitable for the Uppsala larvae and particularly favourable for the Lund larvae. However, given the lack of latititudinal replication both in this and the earlier study, a definitive answer to the question of a latitudinal pattern of differentiation will have to await further research. Finally, recent studies have shown that tadpole morphology responds to the presence of conspecific competitors and this plasticity is supposed to be adaptive (Relyea, 2002). Hence, as we raised tadpoles individually, we do not know how competitive interactions might modify the outcome of the experiments.

An important concern about our study design is the realism of the temperature regimes used in the experiments. Although it is clear that the mean ambient (air) temperatures at the beginning of the breeding season in a given locality tend to increase with increasing latitude across Scandinavia (Cummins, 2003; Laugen *et al.*, 2003b; see also Ståhlberg *et al.*, 2001), whether mean ambient (air) temperatures provides us with a correct picture about the actual temperature regimes experienced by the tadpoles remains unclear. This is because common frogs use a wide variety of breeding habitats both in southern and northern Scandinavia, and there are no data to support the assumption (e.g. Ståhlberg *et al.*, 2001) that the actual temperatures experienced in the north would be higher than those in the south. In fact, in many northern breeding ponds known to us, the average water temperature remains low throughout much of the summer because of an influx of cold snow-melt water, as well as water from cold springs. Also, different ponds and lakes may differ considerably in their thermal environments even within the same region, and therefore the actual thermal regimes faced by growing tadpoles are extremely hard to predict and measure. A further complication is that tadpoles can actively thermoregulate by moving in between shallow and deeper water, and hence any standard measure of ambient or even water temperature does not necessarily relate in any way to the actual temperature regime experienced by tadpoles. Nevertheless, it appears that 10°C as an average growth temperature is too low to be considered as a normal growth environment for common frog tadpoles in Scandinavia. Comparing the length of larval periods in 14 ponds from different parts of Scandinavia to that observed in our laboratory experiments at 14, 18 and 22°C, the appearance of first metamorphs in the wild falls within the time frame which in the laboratory is obtained between 14 and 18°C (Laugen *et al.*, 2003b). Hence, it is likely that the temperatures used by us reflect those seen in the wild.

In summary, we have presented evidence to suggest that the relative length of the tail can indicate the favourability of growth conditions that tadpoles experience: suboptimal temperatures and feeding conditions appear to lead to increased relative tail length simply because of reduced body growth. Our results are also consistent with the proposition that common frog populations across Scandinavia have diverged in their thermal optima for growth, with northern populations being better adapted to grow in warm conditions and southern populations in cooler conditions. However, further studies characterizing the actual thermal environments of growing tadpoles are required before intelligent discussion about thermal adaptation is possible.

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