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Do common frogs (*Rana temporaria*) follow Bergmann's rule?

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ABSTRACT

Questions: Does intraspecific extension of Bergmann's rule – larger size within a species in cooler areas – hold true for ectotherms in general, and for the common frog (*Rana temporaria*) in particular? What is the relative importance of genetic and environmental factors (i.e. direct environmental induction) in determining latitudinal patterns of body size variation in common frogs?

Methods: We tested for a positive association between mean body size and latitude in common frogs (*Rana temporaria*) across a 1600 km long latitudinal gradient in Scandinavia both for wild-collected adults and laboratory-reared metamorphs.

Results: In adults, the mean body size increased from south to mid-latitudes, and declined thereafter. This occurred despite the fact that the mean age of adult frogs increased with increasing latitude, and age and body size were positively correlated. The latitudinal pattern of body size variation in metamorphs reared in a common garden experiment was similar to that observed among wild-caught adults.

Conclusions: The results suggest that the concave pattern of body size variation across the latitudinal cline may be at least partly genetically determined, and that although there is considerable geographic variation in mean body size of *R. temporaria*, this variation does not conform with Bergmann's rule.

Keywords: age, amphibians, body size, cline, growth, latitude, temperature.

INTRODUCTION

According to Bergmann's rule (Bergmann, 1847), endothermic vertebrate species from cooler climates tend to be larger than congeners from warmer climates. This rule was subsequently extended to the intraspecific level to state that races of warm-blooded animals living in colder regions are generally larger than races living in warmer climates (Rensch, 1938;

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Mayr, 1963). Evidence supporting Bergmann's rule in endothermic animals is overwhelming (e.g. Ashton, 2002a; Ashton *et al.*, 2000; Freckleton *et al.*, 2003; Meiri and Dayan, 2003), although the mechanisms underlying the observed patterns remain contentious (e.g. Atkinson, 1994; Angilletta and Dunham, 2003).

Although first formulated for endothermic vertebrates, Bergmann's rule has been shown to apply also to some ectothermic vertebrates (Ray, 1960; Ashton, 2002b; Belk and Houston, 2002; Ashton and Feldman, 2003) and invertebrates (e.g. Cushman *et al.*, 1993; Partridge and Coyne, 1997; Arnett and Gotelli, 1999). However, its general applicability to ectotherms has been questioned, as many ectotherms have been found to follow the converse to Bergmann's rule (decreasing body size with cooler climate) (Park, 1949; Lindsey, 1966; Masaki, 1967; Mousseau and Roff, 1989; Blanckenhorn and Fairbairn, 1995; Mousseau, 1997; Ashton, 2002b; Belk and Houston, 2002). In addition to the controversy regarding the direction of size clines with latitude, there is little consensus as to whether observed latitudinal body size variation in ectotherms is genetically driven, or merely a result of passive phenotypic responses to environmental temperatures (Atkinson, 1994; Barlow, 1994; Van Voorhies, 1996, 1997; Atkinson and Sibly, 1997; Mousseau, 1997; Partridge and Coyne, 1997). Although examples of genetically based body size clines exist (e.g. Gilchrist and Partridge, 1999; Huey *et al.*, 2000), it is a common observation than when reared in low temperatures, most ectothermic animals grow larger than when reared in higher temperatures (Atkinson, 1994; Atkinson and Sibly, 1997; Sota *et al.*, 2000; Blanckenhorn and Hellriegel, 2002).

In a recent meta-analysis, Ashton (2002b) found that most (23/34) amphibian species for which data were available showed latitudinal/altitudinal body size trends consistent with Bergmann's rule. However, opposite patterns were also seen, and the relationship between environmental temperature and body size trends was less clear. For instance, only 7 of 14 anuran species showed patterns concordant with Bergmann's rule, the conclusion being that the 'trends in anurans are tentative' (Ashton, 2002b). Furthermore, none of the studies included in Ashton (2002b) considered latitudinal gradients beyond 55°N. Hence, more case studies – including those from high latitudes – based on high-resolution data are needed to establish the validity of Bergmann's rule in amphibians.

In this study, we investigated patterns of body size variation in the common frog (*Rana temporaria*) along a 1600 km latitudinal gradient (55–69°N) across Scandinavia. In particular, we examined whether body size variation in *R. temporaria* conforms to Bergmann's rule – that is, whether mean body size increases with increasing latitude and/or decreasing temperature. We did this by using three different data sets. First, we investigated adult body size variation using animals collected from 12 different populations in the wild. Second, we raised tadpoles from six different populations in the laboratory until metamorphosis, and compared the patterns of body size variation among adults and juveniles. As metamorphic and adult body size are correlated in amphibians (Smith, 1987; Semlitsch *et al.*, 1988; Berven, 1990; Scott, 1994; Altwegg and Reyer, 2003), the rationale behind this comparison was to establish whether the pattern of body size variation observed in the wild might be genetically, rather than environmentally, determined. Concordant patterns of adult and juvenile body size variation would support genetically driven differentiation, whereas disconcordance would speak for environmental induction. Third, we compared the size of metamorphosing individuals collected from a number of ponds in three geographical areas along the gradient to determine whether the patterns observed are concordant with those observed in the adult and laboratory data. In addition to these comparisons, we employed skeletochronological methods (e.g. Hemelaar, 1985) to establish whether patterns of adult body size variation can be explained by simple differences in populations' age structures.

MATERIALS AND METHODS

Study species

Rana temporaria is the most widespread of the European anurans, and occurs throughout the Fennoscandian peninsula at both high altitudes and latitudes [up to 71°N (Gasc *et al.*, 1997)]. It breeds in a variety of freshwater habitats from temporary ponds to shore marshes of large lakes (Gislén and Kauri, 1959). Several adult life-history traits do show pronounced phenotypic variation over latitudinal and altitudinal clines (Miaud *et al.*, 1999), but detailed studies in geographic variation in adult traits are still lacking (reviewed in Miaud and Merilä, 2000). Several studies have found evidence for genetic differentiation in larval traits (e.g. developmental rate and size at metamorphosis) along latitudinal gradients (e.g. Merilä *et al.*, 2000; Laugen *et al.*, 2002, 2003; Laurila *et al.*, 2002). However, phenotypic plasticity in larval traits is large and even closely situated ponds may differ a great deal in growth and developmental rates (Laurila, 1998; Laugen *et al.*, 2003).

Adult study

Adult *R. temporaria* were captured from 12 populations along a 1600 km transect from southern Sweden to northern Finland in 1998–2000 (Fig. 1; Table 1). The onset of the breeding season in the southernmost and northernmost localities differs by approximately 60 days, and there is a twofold difference in the length of the thermal growth season between the two ends of the gradient (Table 1). Latitude and length of the growth season across this gradient are strongly correlated ($r = -0.99$, $n = 12$, $P < 0.001$), meaning that the latitude itself is a descriptor of temperature gradient as estimated over the activity period in each of the localities. The adults were collected from the spawning ponds at the onset of breeding and transported alive to laboratories in Uppsala and Lund.

Age of individual frogs was determined by counting the number of yearly growth layers (rings) in cross-sections of the second phalange of the right hind leg of a given individual. The rationale behind this method is that in each year a band of bone tissue is formed and bordered by a dark line of arrested growth (Castanet *et al.*, 1977), which can be visualized with standard skeletochronological methods (Hemelaar, 1981, 1985). Cross-sections were photographed with a digital camera fitted to a stereomicroscope, and the number of rings was determined with a light microscope. Details of the ageing methods will be published elsewhere.

Laboratory study of metamorphic size

Tadpoles used in the experiments were obtained using artificial fertilizations as described below. Adults from six of the 12 populations (Table 1, Fig. 1) were used as the parental generation in the laboratory experiment. In most populations, we created 16 maternal half-sib families by crossing each of the eight females with two unique males (16 males in total in each population), whereas in the Umeå population individuals stem from 32 half-sib families (16 females, 32 males). Artificial crosses were not possible in the case of the Ammarnäs population, and eight egg clumps were collected at a breeding site immediately after spawning. Due to the large differences in the onset of spawning among the populations (Table 1), the starting dates for the experiments differed between the

Fig. 1. Map showing the origin of populations used in this study.

Table 1. Descriptive information about the study populations and samples

Population	Latitude (°N)	Longitude (°E)	Altitude (m)	GS (d)*	N_F	N_M	N_P	N_{LF}	N_m
Svartesjöhus	55°30′	13°25′	83	209	8	17	—	—	—
Tvedöra	55°42′	13°26′	22	217	45	45	7	8	545
Farabol	56°26′	14°34′	120	211	1	4	—	—	—
Kärrabol	56°18′	14°33′	130	211	11	19	—	—	—
Hemsjö	56°19′	14°42′	110	211	11	—	—	—	—
Lindrågen	59°28′	13°31′	84	183	14	16	—	—	—
Uppsala	59°51′	17°14′	45	184	32	43	3	8	213
Umeå	63°49′	20°14′	5	158	18	18	—	16	560
Hamptjärn	63°52′	20°13′	62	158	23	23	—	—	—
Ammarnäs	65°54′	16°18′	410	117	21	31	—	8	333
Kiruna	67°51′	21°20′	425	113	36	40	—	8	388
Kilpisjärvi	69°03′	20°47′	485	98	26	31	7	8	422
Total					246	287	17	56	2461

Note: N_F is the number of females and N_M is the number of males collected per population, N_P = the number of ponds followed in the field, N_{LF} = the number of females used in the laboratory experiment, N_m = the number of metamorphosed larvae from the laboratory experiment.

* Length of thermal growth season in days (Alexandersson *et al.*, 1991).

populations. In the southernmost population (Lund) the fertilizations were performed on 9 April 1998, whereas in the northernmost population (Kilpisjärvi) the corresponding date was 4 June 1998. However, the rearing conditions were identical for all populations (see below).

Artificial fertilizations were carried out as outlined in Laugen *et al.* (2002, 2003). One hour after fertilization, eggs were gently detached from the dish and divided into three temperatures treatments [14, 18 and 22°C (± 1°C), two bowls per cross in each temperature], where they were kept until hatching. The water was changed every third day during embryonic development. The eggs collected from nature in Ammarnäs were kept at 14°C until they hatched and then divided into the three different temperature treatments. When the majority of the embryos at a given temperature had reached development stage 25 [hereafter G25 (Gosner, 1960)], eight tadpoles from each cross were placed individually in 0.9 litre opaque plastic containers in each of the two food levels (restricted and *ad libitum*). This procedure was repeated for each population at the three temperatures (14, 18 and 22°C), resulting in 48 experimental tadpoles per cross. 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) every seventh day. The amount of food given to each tadpole was 15 (restricted) and 45 (*ad libitum*) mg for the first week, 30 and 90 mg for the second week, and 60 and 180 mg per week thereafter until metamorphosis. The *ad libitum* amounts were selected to be such that at all temperatures, the tadpoles could not consume all the food before the next feeding. In the restricted food treatment, the tadpoles in the two highest temperature treatments devoured their food resources before the next feeding, indicating food limitation; in the low temperature treatment, however, tadpoles frequently had food left after 7 days. Tadpoles were raised in dechlorinated tap water, aerated and aged for at least 24 h before use, and the water was changed every seventh day in conjunction with feeding. As the rearing of the tadpoles continued from mid-April to late August, we measured temperatures in the laboratories at fixed locations twice a day throughout the experiment to check that the water temperature did not change over time. There was no temperature change over time in any of the laboratories (14°C: $F_{1,122} = 3.87$, $P = 0.051$; 18°C: $F_{1,106} = 0.99$, $P = 0.32$; 22°C: $F_{1,98} = 1.67$, $P = 0.20$).

Field study of metamorphic size

The fieldwork was carried out in 1999 in 17 ponds corresponding to three of the localities used in the adult and laboratory studies (Table 1). Dates for fieldwork were 3 April to 9 July in Lund, 25 April to 15 July in Uppsala and 1 June to 30 September in Kilpisjärvi. After hatching, the ponds were sampled every 7 days in each of the localities. During every visit, we dip-netted the ponds until 20–30 tadpoles were sampled. The tadpoles were killed using MS-222 and stored in 70% ethanol. From each preserved larva, we determined the developmental stage according to Gosner (1960), and tadpoles between developmental stages 38 and 42 were included in the analyses as there was no change in body size after stage 38.

Response variables

The size of adults and field-caught metamorphs was measured as snout–vent length to the nearest 0.01 mm with the use of digital calipers. In the laboratory, we checked containers once a day when larvae approached metamorphosis, and metamorphosed individuals, defined as the emergence of the first foreleg [stage 42 (Gosner 1960)], were removed from the containers and weighed with an electronic balance to the nearest 0.0001 g. Because of time constraints, metamorphs from the laboratory study were not measured for snout–vent length.

Statistical analyses

Variation in adult size was analysed with general linear models as implemented in PROC MIXED of the SAS 6.12 statistical package (Littell *et al.*, 1996). In the full model, we included sex as a fixed factor and population of origin as the random factor (to control for non-independence of individuals). Latitude, altitude, the square of latitude and age were included as covariates.

The size of field-caught metamorphs was analysed with a nested analysis of variance (ANOVA) using PROC MIXED in SAS (Littell *et al.*, 1996). Geographical area was included in the model as a fixed effect and individual ponds (random effect) were nested within area.

The laboratory experimental design was a $6 \times 3 \times 2$ factorial ANOVA with population (six levels), temperature (14, 18 and 22°C) and food level (*ad libitum*, restricted) as factors. The mean weight of two maternal half-sib families was used as the response variable, the sample size for each treatment combination being eight in most populations, except in Umeå where 16 females were used. General linear model analysis of covariance as implemented in PROC GLM in SAS was used to identify the sources of fixed effect variation in metamorphic size. Temperature and food level treatments were treated as fixed effects, while latitude of origin in each population as well as the squared latitude term were fitted in the model as covariates. Response variables in the laboratory experiment were log-transformed before the analyses to meet the assumptions of normality and homogeneity of variances. However, for the ease of interpretation, graphed means and standard errors are given in the original scale. Curve fit regressions for the figures were tested using PROC GLM in SAS (results not shown).

RESULTS

Adult size

An initial analysis of adult snout–vent length indicated that none of the possible two-way interactions between latitude, latitude^2, altitude and sex were significant ($F_{1,512} \geq 2.18$, $P \geq 0.14$). Therefore, the analysis was limited to an evaluation of the main effects only. While the effect of altitude was not significant (Table 2), both the latitude and latitude^2 terms explained significant amounts of variation in the mean body size of adults (Table 2; Fig. 2a). The mean snout–vent length of adults increased from the southernmost population at 55°N to Umeå (64°N), declining thereafter in the three northernmost populations (Fig. 2a). As indicated by the significant sex effect (Table 2), females were in general larger than males (Fig. 2a). The results and the inference were largely the same even if individual age was included in the model as a covariate (Table 2; Fig. 2b). In other words, the latitudinal patterns of body size variation cannot be explained by latitudinal variation in population age structure.

Table 2. General linear mixed-model analyses of adult body length in 12 *Rana temporaria* populations (a) without and (b) with age as a covariate

Source	(a) Age not accounted for		(b) Age accounted for	
Random effects	var. ± SE	*z*	var. ± SE	*z*
Population	7.57 ± 4.27	1.77*	7.15 ± 4.08	1.75*
Residual	31.62 ± 1.96	16.13***	28.81 ± 1.79	16.10***
Fixed effects	d.f.	*F*	d.f.	*F*
Latitude	1	7.44**	1	5.90*
Latitude^2	1	6.69*	1	5.35*
Altitude	1	0.02	1	0.85
Sex	1	32.49***	1	29.57***
Age	—	—	1	53.23***

Note: var. = variance component, SE = standard error, d.f. = degrees of freedom. *$P < 0.05$, ***$P < 0.001$.

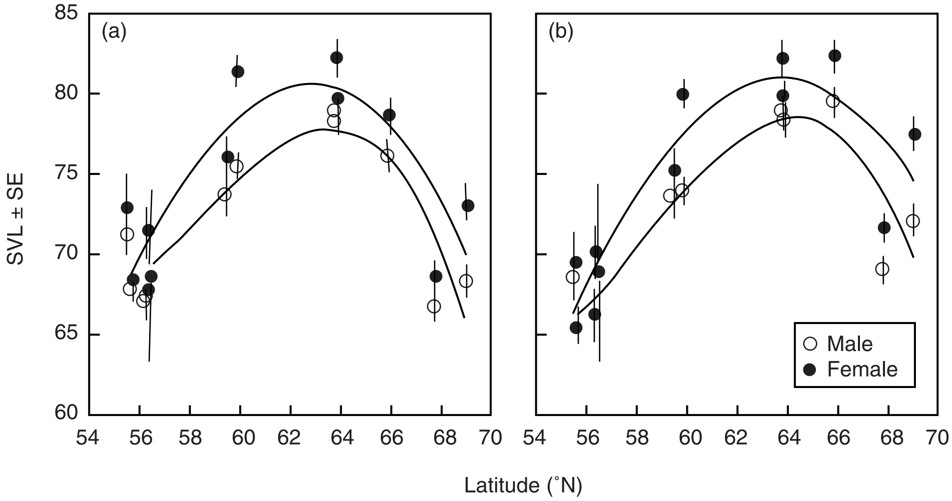

Fig. 2. Mean adult size (snout–vent length, SVL ± standard error) of male and female *Rana temporaria* as a function of latitude (a) without accounting for and (b) accounting for age effects. In (b), the depicted values are least square means (± standard error) accounting for effects of variation in population age structure.

Size at metamorphosis in the laboratory

Body size of the laboratory-reared metamorphs was not ordered in a linear fashion with latitude (Table 3, Fig. 3a,b). Instead, the relationship between size and latitude was curvilinear, with metamorphs from the mid-latitude populations being larger than those from the southern and northern edges of the gradient (Fig. 3a,b). Temperature had a profound effect

Table 3. Results of analysis of covariance for size at metamorphosis in the laboratory experiment

Source	d.f.	MS	*F*
Latitude	1	1.14	255.48***
Latitude^2	1	1.14	255.91***
Temperature	2	0.06	14.01***
Food	1	16.24	3647.12***
Latitude × Temperature	2	0.07	15.58***
Latitude^2 × Temperature	2	0.07	16.09***
Error	1058	0.00	
Model	9	3.94	886.36***

*** $P < 0.0001$.

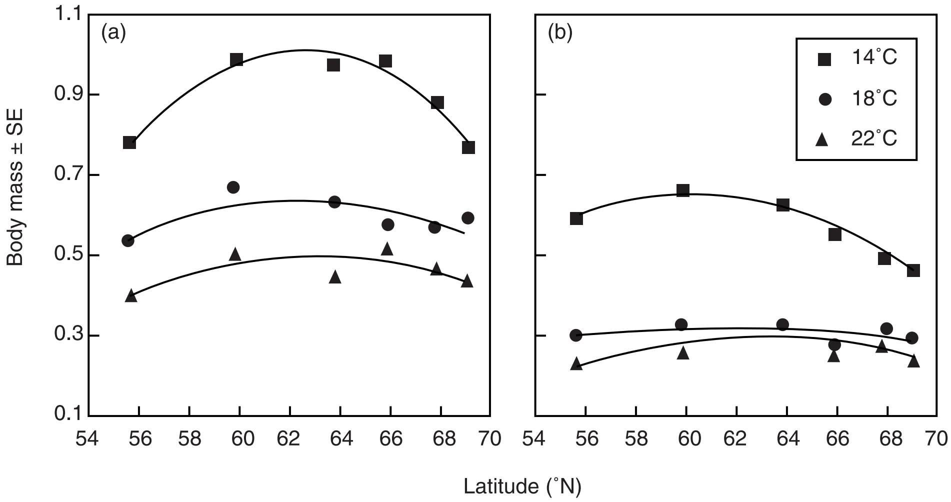

Fig. 3. Mean size (body mass ± standard error) of laboratory-reared *Rana temporaria* metamorphs in different treatment conditions as a function of latitude of origin. (a) *Ad libitum* food level, (b) restricted food level.

on metamorphic size (Table 3): in all populations, tadpoles were clearly largest at 14°C and smallest at 22°C (Fig. 3a,b). However, the reduction in size was much smaller from 18 to 22°C than from 14 to 18°C (Fig. 3a,b). As indicated by significant latitude × temperature and latitude^2 × temperature interactions (Table 3), the reaction norms for size in response to temperature treatments differed among the populations. For instance, the amplitude of the temperature-induced changes was much narrower for the tadpoles from the most northern locality (Kilpisjärvi) than for the tadpoles from the central populations (Fig. 3a,b). Size was also strongly influenced by the food treatment (Table 3), with the tadpoles in the *ad libitum* food treatment attaining almost twice the size of those in the restricted food treatment (Fig. 3a,b).

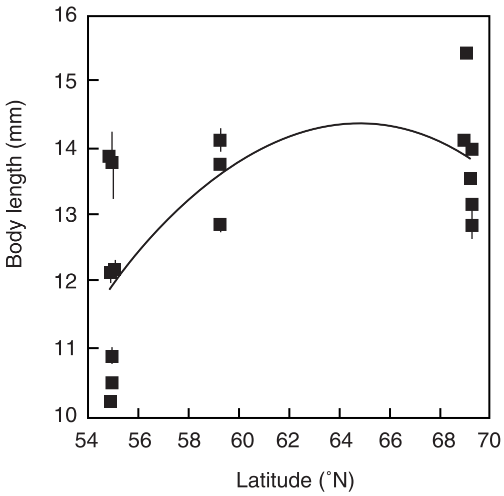

Fig. 4. Mean body length (± standard error) of field-caught *Rana temporaria* metamorphs as a function of latitude. Each dot represents a mean of a distinct pond.

Concordance between adult and laboratory data

To determine whether the latitudinal body size trends in the adult and laboratory data sets were concordant, we used mean metamorphic size in the laboratory (only in the *ad libitum* food treatment) as a response variable in a general linear model treating mean adult size as a covariate and temperature treatment in the laboratory as a factor. A significant positive ($b = 0.0087 \pm 0.0025$) relationship between metamorphic and adult size ($F_{1,14} = 11.83$, $P = 0.004$) was observed. While temperature again had a highly significant effect on metamorphic size, there was no significant interaction between adult size and temperature treatment ($P > 0.05$).

Size at metamorphosis in the field

The mean body size of field-caught metamorphs differed between the three geographical areas ($F_{2,14.4} = 5.21$, $P = 0.0199$), as well as between subpopulations within each area ($Z = 2.49$, $P = 0.0064$; Fig. 4). Although mean body length was positively correlated with latitude across the populations ($r_s = 0.58$, $n = 17$, $P = 0.0142$; Fig. 4) in accordance with Bergmann's rule, lack of samples from mid-latitudes makes direct comparisons with the adult and laboratory data sets difficult.

DISCUSSION

Body size trends

The results of the present study do not give unequivocal support to the contention that geographic variation in body size in *R. temporaria* conforms to Bergmann's rule. While the mean body size of both wild-caught adults and the laboratory-reared metamorphs was an increasing function of latitude until about 65°N, the mean body size declined markedly thereafter towards higher latitudes. While the mean body size of the field-collected metamorphs was a positive function of the latitude, data from mid-latitude populations – where the adult body size peaked – was lacking. Consequently, it is possible that the same concave pattern of body size variation as observed in adults would have emerged with denser latitudinal sampling of metamorphs from the field. Interestingly, all other studies focusing on latitudinal or altitudinal body size trends in amphibians (reviewed in Ashton, 2002b), and in *R. temporaria* in particular (Elmberg, 1991; Miaud *et al.*, 1999), have considered populations at latitudes below 65°N. As pointed out previously (e.g. Ashton and Feldman, 2003), the magnitude and direction of body size trends may vary with latitude. This may explain why previous studies (Elmberg, 1991; Miaud *et al.*, 1999) of latitudinal/altitudinal body size clines in *R. temporaria* found positive correlations between mean body size and latitude/altitude. However, it is worth noting that the study of Elmberg (1991) included only three populations, whereas the altitudinal trend in Miaud *et al.* (1999) was significant only for males, not for females. Furthermore, the positive trend reported by Miaud *et al.* (1999) is due mainly to a difference between populations originating from altitudes below or above 500 m – there are no altitudinal trends in mean body size at either side (i.e. 0–500 m vs. 500–2400 m) of this point (Miaud *et al.*, 1999; see also Figure 2f in Ashton, 2002b). Hence, we conclude that the evidence for the application of Bergmann's rule in *R. temporaria* is, at best, weak: it may be a valid descriptor of body size trends over shorter geographic distances, but not when longer altitudinal or latitudinal gradients are considered. Rather, our results parallel those of Geist (1986) for some large mammals (deer, wolf) in North America. As in the present study, Geist (1986) found that maximum body size along a latitude gradient occurred between 53 and 65°N, with smaller body sizes at both lower and higher latitudes.

Mechanisms

How can we explain the concave pattern of body size variation over the latitudinal gradient observed in this study? Several different explanations are possible.

First, the observed latitudinal pattern of adult body size variation could simply reflect an underlying pattern of variation in population age structure. This has been suggested to account – at least partially – for differences in the mean body size of lowland and mountain populations of common frogs (Ryser, 1996; Miaud *et al.*, 1999). However, since our analyses controlled for age effects, differences in populations' age structure cannot explain latitudinal body size patterns observed in our data.

Second, it has been recognized for some time that ectotherms reared under low temperatures tend to grow larger than those reared under higher temperatures (Atkinson, 1994). This is also what we found: size at metamorphosis was clearly a decreasing function of temperature in all populations and at both food levels in the laboratory experiment. Hence, if the average temperatures experienced by growing individuals are lowest at mid-latitudes, then the concave pattern of latitudinal body size variation in metamorphs and adults could be explained by simple environmental induction. However, since the length of the growth season declines linearly with latitude across Sweden (see Methods), this explanation can also be rebuffed. However, it is worth highlighting that the average ambient temperature over the 90 day period of larval growth from hatching to metamorphosis across the latitudinal gradient considered here is not a linear function of latitude. Instead, like the observed latitudinal body size patterns (cf. Figs. 2 and 3), average temperatures follow a concave latitudinal pattern (see Figure 2 in Laugen *et al.*, 2003). Hence, if we assume that the temperatures during the early growth and developmental period are important for the determination of adult body size, then our data would actually suggest the converse to Bergmann's rule with respect to temperature (correlation between adult body size and mean temperature [from Laugen *et al.* (2003) and The Swedish Meteorological and Hydrological Institute] over the 90 day period of early development: $r_s = 0.67$, $n = 11$, $P = 0.02$ [males]; $r_s = 0.52$, $n = 12$, $P = 0.08$ [females]). Since several studies have found that individual variation in body size established at metamorphosis tends to persist throughout life (Smith, 1987; Semlitsch *et al.*, 1988; Berven, 1990; Scott, 1994; Altwegg and Reyer, 2003), it is not unthinkable that the temperatures experienced during the early breeding season could provide an explanation for the concave pattern of latitudinal body size variation seen in this study. This explanation is similar to that put forth by Geist (1986): he proposed that the concave latitudinal body size pattern observed in some mammals was causally linked to the length of the 'productivity pulse', which should peak at intermediate northern latitudes.

Turning to more complex explanations, there is good evidence that selection stemming from the decreasing length of the growth season from south to north has favoured faster larval development in the north: the length of the larval period in a common environment was a linearly declining function of latitude along the gradient considered in this study (Laugen *et al.*, 2003). Since increased rate of development occurs at the cost of smaller body size at metamorphosis (Laurila *et al.*, 2002), one would expect the mean body size at metamorphosis to be a declining function of latitude. Since this is obviously not the case (see Fig. 3), this suggests that strong positive selection for large size at metamorphosis in the northern populations (at least until 65°N) has been necessary to compensate for the expected body size reduction due to accelerated development. However, the lack of such compensation in the northernmost populations could be due to the harsh environmental constraints resulting from the extremely short growth season. For instance, selection in the northernmost populations might favour allocation of resources to energy stores, rather than further growth, to sustain long (about 8 months) hibernation. In other words, as with insects, in which constraints on available larval development time have been identified as a factor producing the converse to Bergmann's rule (Mousseau, 1997), we see time constraints as a possible key for understanding the small body size of the common frogs in the two northernmost populations.

If large metamorphic size is beneficial in the absence of time constraints, why do the southern tadpoles metamorphose at smaller size? Size at metamorphosis is predicted to reflect the balance between growth opportunities and survival between the aquatic and terrestrial habitats (Werner, 1986; Rowe and Ludwig, 1991). We suggest that the answer may lie in the relatively low growth rates (Laurila *et al.*, 2001; Laugen *et al.*, 2002) and, possibly, more favourable growth conditions in terrestrial habitats in the southern latitudes favouring metamorphosis at smaller size.

Finally, although the original explanation for Bergmann size clines – more efficient heat conservation in larger bodied animals – is not generally considered valid in ectotherms, it is possible that small body size can provide a thermal advantage in cold climates by allowing more accurate thermoregulation (Asthon, 2002b), for example by more rapid heat gain (Cushman *et al.*, 1993). Furthermore, Ashton (2002b) suggested that precipitation and humidity could be important selective factors behind latitudinal and altitudinal body size trends in adult amphibians. Since large individuals have better desiccation tolerance than smaller individuals (e.g. Newman and Dunham, 1994), this could select for large body size in dry environments. While we cannot refute the possibility that the observed pattern of latitudinal body size variation in this study could at least partly be related to demands dictated by the thermal environment, we consider differences in precipitation an unlikely explanation. Namely, differences in yearly precipitation are not very great along the present gradient [488–726 mm (Alexandersson *et al.*, 1991)] and there is no correlation between adult body size and amount of precipitation in a given locality (males: $r = -0.04$, $P = 0.90$; females: $r = -0.12$, $P = 0.59$), suggesting that variation in precipitation is not an important factor determining adult body size distribution in this case.

Environmental or genetic determination of body size trends?

For good reasons, many authors have recently questioned whether latitudinal and altitudinal body size trends in the wild are environmentally rather than genetically driven (e.g. Atkinson, 1994; Van Voorhies, 1996, 1997; Atkinson and Sibly, 1997; Mousseau 1997; Partridge and Coyne, 1997). To this end, relevant studies of amphibians are few and far between. Berven *et al.* (1979) and Berven (1982a) found that tadpoles from mountain populations were larger than lowland tadpoles in natural ponds, but that these differences diminished or even reversed when the tadpoles were raised in common garden experiments. Hence, the larger body size in mountain ponds was mostly a plastic response to low temperature. In a transplant study, Berven (1982b; see also Bernardo, 1994) concluded that differences in size at maturity between mountain and lowland populations of *R. sylvatica* had a genetic basis, although his analyses did not account for the initial differences in body size of the transplanted juveniles. In the present study, we found a positive correlation between the mean body size of wild-caught adults and laboratory-reared juveniles. Providing that metamorphic and adult body sizes are positively correlated in the wild, these results suggest that the latitudinal body size patterns in adult *R. temporaria* could be genetically driven.

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