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Length of activity season drives geographic variation in body size of a widely distributed lizard

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Abstract

Understanding the factors that drive geographic variation in life history is an important challenge in evolutionary ecology. Here, we analyze what predicts geographic variation in life-history traits of the common lizard, *Zootoca vivipara*, which has the globally largest distribution range of all terrestrial reptile species. Variation in body size was predicted by differences in the length of activity season, while we found no effects of environmental temperature per se. Females experiencing relatively short activity season mature at a larger size and remain larger on average than females in populations with relatively long activity seasons. Interpopulation variation in fecundity was largely explained by mean body size of females and reproductive mode, with viviparous populations having larger clutch size than oviparous populations. Finally, body size-fecundity relationship differs between viviparous and oviparous populations, with relatively lower reproductive investment for a given body size in oviparous populations. While the phylogenetic signal was weak overall, the patterns of variation showed spatial effects, perhaps reflecting genetic divergence or geographic variation in additional biotic and abiotic factors. Our findings emphasize that time constraints imposed by the environment rather than ambient temperature play a major role in shaping life histories in the common lizard. This might be attributed to the fact that lizards can attain their preferred body temperature via behavioral thermoregulation across different thermal environments. Length of activity season, defining the maximum time available for lizards to maintain optimal performance, is thus the main environmental factor constraining growth rate and annual rates of mortality. Our results suggest that this factor may partly explain variation in the extent to which different taxa follow ecogeographic rules.

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Introduction

Species distributed across broad geographic ranges often exhibit extensive variation in life-history traits, and understanding the causes and consequences of this variation has been a central topic in evolutionary ecology for decades. Environmental factors that exert strong effects on animal life histories include food availability (Ballinger 1977; Yom-Tov et al. 2006; Naya et al. 2007), rainfall (Blois et al. 2008; Marquis et al. 2008), and population density (Massot et al. 1992; Jenkins et al. 1999). However, most attention has focused on the effect of temperature (Adolph and Porter 1993; Atkinson 1994; Gotthard 2001; Adams and Church 2008; Angilletta 2009), largely due to the fact that temperature directly impacts on many aspects of the physiology and behavior of organisms (Angilletta 2009). For example, one of the most recognized ecogeographic rules, Bergmann's rule, predicts evolution of larger body size in colder environments as a result of enhanced ability to conserve heat (Bergmann 1847). Although Bergmann's rule was originally conceived for endotherms (mammals and birds), with focus on interspecific comparison, some groups of ectotherm taxa show clear geographic clines in body size that are consistent with Bergmann's rule (intraspecific examples: Arnett and Gotelli 1999; Ashton 2001; Ficetola et al. 2010; interspecific examples: Cushman et al. 1993; Cruz et al. 2005; Olalla-Tárraga et al. 2006; for discussion see Olalla-Tárraga 2011 or Meiri 2011). On the other hand, several ectotherms show the opposite pattern, that is, smaller body size in cooler environments (Lindsey 1966; Ashton and Feldman 2003; Olalla-Tárraga et al. 2006; Cvetković et al. 2009). The selective regimes that drive these patterns are not fully understood and may include other aspects of the environment than ambient temperature. This is particularly relevant for studies that rely on latitude as a proxy for temperature (e.g. Ashton and Feldman 2003; Cruz et al. 2005; Pincheira-Donoso et al. 2008), because latitude may correlate with several abiotic and biotic factors that generate selection on body size (Hawkins and Diniz-Filho 2004). For example, it has been shown that environmental productivity (Rosenzweig 1968) or environmental seasonality (Murphy 1985; Meiri et al. 2005) can drive body-size patterns, possibly by affecting food availability across climatic gradients. Furthermore, as most ectotherms grow larger when reared at lower temperatures (Atkinson 1994; Partridge et al. 1994; Van Voorhies 1996; Angilletta and Dunham 2003), Bergmann clines may at least partially arise as a result of general plastic response in cell size (Van Voorhies 1996).

Adaptive explanations for geographic variation in life-history traits mainly focus on how temperature and other factors mediate costs and benefits of growth and therefore the optimal age and size at maturity (Berrigan and Charnov 1994; Kozlowski et al. 2004; Arendt 2011). As regards temperature, most ectotherms grow slower and attain larger final body size in colder environments, which is achieved by prolonging growth and delaying maturation (Morrison and Hero 2003). Optimality models predict evolution of larger body size in cool environments if the cost of reduced survival to maturity can be offset by, for example, a larger increment in fecundity or improved survival (Kozlowski et al. 2004; Arendt 2011). When growth rates are lowered by reductions in food, age and size at maturity respond in the opposite way, that is, animals mature later at a smaller size (Berrigan and Charnov 1994).

Although temperature has a direct influence on different aspects of behavior and physiology of ectotherms, some species including many lizards, are active thermoregulators that use various behavioral mechanisms to maintain relatively constant body temperatures during activity (e.g. Bauwens et al. 1996). Thus, individuals inhabiting warmer environments do not necessarily exhibit higher body temperatures compared to individuals from colder environments (Castilla et al. 1999). However, there is substantial variation across climatic regimes in the amount of time that a lizard can be active at its preferred body temperature (Adolph and Porter 1993). Activity times determine how much energy will be allocated to growth or reproduction (e.g. Niewiarowski 2001) as most processes which are linked to energy acquisition and energy assimilation are highly temperature dependent and both are being maximized at preferred body temperature (Avery 1971; Van Damme et al. 1991). Individuals with longer activity season are therefore expected to grow faster and attain maturation at smaller size and earlier age (Adolph and Porter 1993; Sears 2005). Thus, in lizards, selection on age and size at maturation imposed by the thermal environment could arise through its effect on activity times and not through temperature per se (Adolph and Porter 1993; Sears and Angilletta 2004; Olalla-Tárraga et al. 2006; Olalla-Tárraga 2011). However, whether geographic variation in body size can be explained by variation in activity patterns has rarely been tested (but see Sears and Angilletta 2004; Sears 2005; Olalla-Tárraga et al. 2006).

Our aim in this study was to conduct a spatially and phylogenetically controlled analysis of the drivers of geographic variation in body size and fecundity, and their relationship, in the common lizard, *Zootoca vivipara* (Lichtenstein, 1832). The common lizard (Fig. 1) is a very suitable system for addressing this issue because its phylogeography is relatively well understood (Surget-Groba

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Figure 1. Female common lizard (*Zootoca vivipara*) from viviparous population in Slovakia with freshly laid eggs. The fully developed juveniles hatch within few hours to 1 day. Photograph David Jandzik.

et al. 2001, 2006) and it has the widest geographic range of all terrestrial reptiles, occurring from Ireland in the west to Japan in the east and from southern Spain to northern Scandinavia (see Fig. 2 and Table A1; Dely and Böhme 1984). We specifically focused on testing whether (1) differences in seasonal activity better explain variation in body size than differences in mean ambient temperature experienced during activity; (2) costs associated with higher growth rates (longer seasonal activity) are offset by some benefits (e.g. improved fecundity or survival; Arendt 2011); (3) other abiotic factors which have an effect on growth rate (e.g. via food availability) significantly contribute to variation in body size; (4) the potential costs of higher growth rate are offset by benefits in terms of fecundity or survival at the population level.

Material and methods

The common lizard is a small lacertid lizard (adult body length varies between 40 and 80 mm in snout-vent length; SVL) occurring throughout much of Europe and Asia. It mainly inhabits humid habitats and can be found from sea level up to altitudes of about 2500 meters. It is one of the few reptiles exhibiting reproductive bimodality, with oviparous populations restricted to some areas in South-Western and South-Eastern Central Europe (e.g. Heulin and Guillaume 1989; Mayer et al. 2000). Females usually reproduce once a year, but can lay multiple clutches in some populations. This is true for most oviparous populations in which females commonly lay one to three clutches per season and rarely for some lowland viviparous populations, in which females occasionally produce two clutches (Patrick S. Fitze, unpubl. data). The reproductive cycle follows a consistent pattern with mating and ovulation in spring, and the young are born in mid to late summer. The lizards enter hibernation in autumn, usually in September or October.

Data collection

In total, we gathered life-history data from 64 oviparous and viviparous populations (3677 specimens) of the common lizard throughout its range (Fig. 2 and Table A1). We obtained data on various life-history traits from our own field studies or from other researchers (see Table A1 for the full list). The life-history parameters assembled here are the minimum (smallest female in the sample), maximum (largest female in the sample), and mean (arithmetic) body size (SVL) of adult females (adulthood is based on observed reproductive status of wild-caught females), minimum age at first reproduction (assessed either by skeletochronology or mark-recapture), mean (arithmetic) fecundity (clutch size), and the slope of the regression of fecundity on body size. The last describes how fecundity increases with body size within each population, which is an important component of life-history models predicting the age and size at maturity (e.g. Arendt 2011). If oviparous females produced two clutches per season, we used the average value in all analyses (the second clutch is usually smaller in studied populations, see Heulin 1988; Heulin et al. 1991).

We included only studies which met the following criteria: (i) minimum number of adult females per population was seven; (ii) populations or individual females were not experimentally manipulated; (iii) it was possible to use each population as an individual data point. If the same population was repeatedly recorded in more than one study, we calculated an average for each trait for that population. Due to the small subset of populations for which the data on age at reproduction was available, we excluded this variable from our analyses (but see Table S1 for original data). Instead we chose to include minimum body size, which is considered to better predict sexual maturation in this species (Bauwens and Verheyen 1987).

Elevation data were obtained directly from the published papers or estimated from WordClim at a spatial resolution 10 arcminutes (http://www.worldclim.org/) using reported geographic coordinates. Climatic variables considered were mean temperature during the activity season and mean precipitation during the warmest quarter of the year. Data on temperature and rainfall were obtained from WorldClim and IWMI Climate Atlas Web Query service (http://wcatlas.iwmi.org/Default.asp), which

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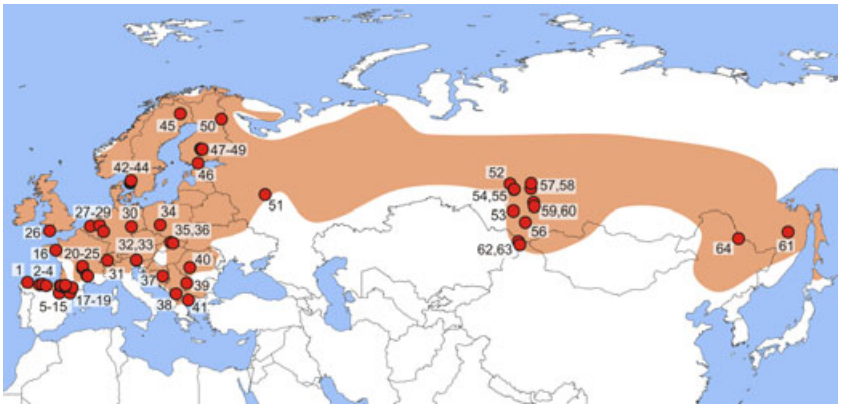

Figure 2. Map showing the range of the common lizard (*Zootoca vivipara*; in ochre color) and localities of the populations used in this study. For details on localities and source of the data see Table A1.

provide available data for 40–50 years for each population. We chose mean precipitation as an additional predictor of variation in body size and fecundity because it is a major predictor of the distribution of the species (Dely and Böhme 1984) and because precipitation is generally considered to correlate with environmental resource abundance (Lorenzon et al. 2001; Marquis et al. 2008). It also captures annual variation in rainfall during the majority of gestation and has been shown to correlate with within-population variation in reproductive output and survival (Marquis et al. 2008). Many studies that analyze geographic variation in life history use annual mean temperature (e.g. Ashton and Feldman 2003; Adams and Church 2008), which does not reflect the temperature during the relevant period of lizard activity as it includes winter, during which common lizards hibernate underground. We therefore used the mean temperature during activity season, which was calculated for each population as the mean of the monthly mean temperatures during the period of female activity. However, annual temperature correlates with the length of activity season, with emergence dates usually corresponding to an average air temperature of 8°C across the geographic range of the species. The length of activity season is a potentially important factor that influences opportunity, costs and benefits for growth that correlate with climatic regimes in ectotherms (e.g. Gotthard 2001). Furthermore, the length of activity season is considered to be positively correlated with mortality risk in lizards (Adolph and Porter 1993). We therefore extracted this information from published accounts or via personal observations from field work. Because there may be substantial annual variation in emergence and hibernation dates, we calculated activity season for each population according to the average date of female emergence and hibernation, with a precision of a half months, that is, we split each month into halves (e.g. the first of April to mid-April, mid-April to the end of April etc.). The full dataset is available as the online supporting information (Table S1).

Phylogenetic framework

For the analysis of phylogenetic relationships between populations we used 1649 bp fragments of mitochondrial DNA sequences of cytochrome *b* (1168 bp) and 16S rRNA (481 bp) genes published by Surget-Groba et al. (2006) (GenBank accession AY714882-AY714981). Haplotypes were assigned to populations based on sampling location, our own sequence data, and information linking the haplotypes with localities in Surget-Groba et al. (2001, 2006; provided by Yann Surget-Groba). For localities where more haplotypes were found or the assignment was ambiguous, we used degenerate consensual sequence of all haplotypes that occur or might potentially occur there. The best-fit model of sequence evolution was selected by Akaike information criterion as implemented in jModeltest 0.1.1 (Posada 2008). The phylogeny was reconstructed using maximum likelihood optimality criterion implemented in PhyML 3.0 (Guindon et al. 2010) with the best approach combining nearest neighbor interchanges with subtree pruning and regrafting algorithm and using the TIM2 + G + I model of sequence evolution. Branch support was quantified as bootstrap values (based on 100 resampled datasets) as well as approximate likelihood ratio test (aLRT) using Shimodaira-Hasegawa-like procedure implemented in PhyML 3.0. The resulting tree (Fig. A1) showed basically the same topologies as previously published by Surget-Groba et al. (2001, 2006) with the exception of sister relationship of the clades B + D instead of D + E; however, this had low branch support. We also conducted neighbor-joining phylogenetic analysis with short fragments of cytochrome *b* to obtain the same topology of the branches as in the older phylogeny published by Surget-Groba et al. (2001) (data not shown). This phylogeny is less controversial as it suggests only one evolutionary origin of viviparity instead of two or reversal to oviparity from viviparity as suggested by the phylogeny based on Surget-Groba et al. (2006) as well as by our maximum likelihood analysis.

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Comparative analyses

Comparisons across populations may be confounded by the spatial distributions of observations. Spatial autocorrelation occurs when observations originating from nearby locations are more similar to each other than to those drawn from more distant locations (Dormann et al. 2007). In addition, closely related populations can be more similar to each other than is expected by chance because of shared evolutionary history (Harvey and Pagel 1991). To control for the potentially confounding issues of phylogenetic and spatial autocorrelation, our first approach was to use a regression model capable of accounting for both sources of non-independence simultaneously within a single statistical framework (Freckleton and Jetz 2009). This method, based on phylogenetically independent contrasts, incorporates two parameters, λ (Pagel 1999) and ϕ (Freckleton and Jetz 2009), which, respectively, account for the extent of phylogenetic and spatial autocorrelation present in the residual variation in a given regression model. Practically, these parameters are estimated simultaneously by maximum likelihood methods (see Freckleton and Jetz 2009 for details), and, once estimated, it is possible to derive additional metrics to describe the relative sources of variance in a given model. The first is simply ϕ, which can vary from zero (no spatial effect) to one (all trait variance explained by geographic distance). The second is λ', a spatially corrected version of λ, which also varies between zero (traits are independent of phylogeny) and one (trait variance follows a Brownian motion model of evolution). The final metric is γ, which measures the proportion of model variance not attributable to either geography or space. As ϕ, λ', and γ sum to one representing total variation, the relative magnitudes of the three parameters give an indication of the extent of non-independence in a given model, and the balance between the potential components of nonindependence. As a contrast, we ran a second set of models without correction to provide a better insight on the effects of space and phylogeny in our first models sets.

To determine the best combination of predictors of each life-history trait, we used an information theoretic approach (Burnham and Anderson 2002) based on Akaike information criteria (AIC) scores, corrected for small sample size (second-order AIC = AIC_c). The benefit of using this approach is that we can assess the relative importance of models of varying complexity without many of the problems associated with model simplification procedures (e.g. increased Type I error rates). Within each life-history trait, we restricted the dataset to include only those populations for which we had data for each variable. In addition, in the spatial-phylogenetically controlled analyses we used only those populations for which we had genetic data, and trimmed the tree accordingly. Prior to model fitting, we also standardized all predictor variables to have a mean of zero and SD 0.5; standardizing predictors in this way facilitates the interpretation of the relative strength of effect sizes for both continuous and categorical predictors after model averaging (Gelman 2008; Grueber et al. 2012). Using this dataset we then fitted models encompassing all possible combinations of predictor variables, including a null (intercept-only) model, calculating for each combination the AIC_c score of the model. Multicollinearity is a potentially significant issue in multiple regression modelling, as a linear relationship between two (or more) predictor variables can result in an inflation of the variance associated with parameter estimates. However, we avoid most the issues associated with multicollinearity by employing a method based on multimodel inference, which considers all possible combinations of predictor variables (Graham 2003). Nonetheless, we decided to explore the extent of multicollinearity in our dataset by calculating variance inflation factors (VIFs) for the full set of predictors in each model set to determine the extent to which the variance around each estimate is increased by collinearity. The results of this analysis (Table A2) indicated moderate multicollinearity between latitude and altitude and other predictor variables, with VIFs consistently >2. Although our method of model inference is likely to be robust to this level of multicollinearity as mentioned above, latitude and altitude are predictors with no direct biological value (in contrast to the remaining life history-related predictors). Therefore, we also used an alternative dataset in which these two predictors were excluded. This simultaneously eliminates the risk that latitude and altitude would do the following: (i) obscure the true relationships between life history-related traits and environmental conditions and (ii) confound model inference due to issues associated with multicollinearity.

To identify the model(s) providing the most parsimonious fit, we ranked models by their AIC_c scores. To assess the likelihood that a particular candidate model is the best model, we also calculated the Akaike weight of all candidate models (Burnham and Anderson 2002). Because in some cases there was no single model that performed substantially better than other models and in order to assess the relative importance of individual predictors, we calculated parameter importance as the sum of Akaike weights of all models that included the parameter of interest (Burnham and Anderson 2002). To assess the impact of spatial and phylogenetic correction on our results, we repeated the modelling procedure using linear models without correction. As reproductive mode turned out to be a strong predictor of life histories in the common lizard (see below), we repeated all analy-

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ses with dataset of the viviparous populations only (small sample size prevented us from analyzing oviparous populations separately). All analyses were conducted in R v. 2.13.0 (R Development Core Team 2011) using code written by R. Freckleton and the AICcmodavg package (Mazerolle 2013).

Results

The common lizard shows substantial geographic variation in body size and reproductive output (see Table S1). The results for analyses including latitude, altitude, and climatic variables are summarized in Table 1, while Table 2 shows the results for climatic variables only. In spatial-phylogenetically controlled model sets (Tables 1A, 2A) the relative importance of the best predicting variables consistently reaches higher values than in model sets with no correction (Tables 1B, 2B) suggesting substantial spatial and phylogenetic effects, and we therefore focus on the results for this set of analyses (i.e. those presented in Tables 1A, 2A). Spatial autocorrelation explains more variance than phylogenetic autocorrelation in all models except for the models of SVL-fecundity regression slope where the effect is more equally distributed (compare λ and ϕ in Table S2 sheets A, B, E, and F).

The relatively most important predictor of variation in average SVL among populations is the length of activity season, with lizards being larger in populations with shorter activity season (Tables 1A, 2A; Fig. 3). There is no support for an effect of temperature, latitude or altitude (Table 1A, B). These results are very similar for minimum and maximum body size, with an added effect of precipitation (larger size in wetter regions; Tables 1A, 2A). The relative importance of the length of activity season effect on body size is similar or strengthened in the case of minimum SVL in the dataset excluding latitude and altitude (compare Tables 1A and 2A).

The best predictor of clutch size is body size, followed by reproductive mode, with lizards from viviparous populations having larger relative fecundity (for given SVL) than those from oviparous populations (5.94 ± 0.18 SE vs. 4.65 ± 0.3 SE). Viviparous populations also show a steeper increase in fecundity with increasing body size than did oviparous populations, with minor contributions of the length of activity season and latitude (Tables 1, 2).

The results for the analyses of viviparous populations only (see Table A3) did not significantly change the overall results.

Discussion

Our analyses showed that geographic variation in body size of the common lizard can largely be explained by differences in the length of activity season rather than the temperature experienced during the active part of the year. The lack of support for an effect of temperature is likely because lizards are capable of behavioral thermoregulation, which means that body temperatures are not simply caused by passive heat fluxes, but rather reflect behavioral selection of thermal environments (Olalla-Tárraga et al. 2006; Olalla-Tárraga and Rodríguez 2007). Indeed, the common lizard shows strong evolutionary conservation of preferred body temperature across its geographic range (review in Castilla et al. 1999; Uller and Olsson 2003). Of greater importance is therefore the amount of time lizards spend at their preferred body temperature as processes linked to the energy acquisition (e.g. sprint speed, prey encounter rate, gut-passage rate, food digestion) are maximized at this temperature (Avery 1971; Van Damme et al. 1991). Because the rate and duration of somatic growth determine when sexual maturity is reached, females that are active for a higher number of days should grow more per year and may mature sooner at a smaller size (Adolph and Porter 1993). On the other hand, growth is costly and females from time-constrained environments may be selected to grow faster to reach minimum reproductive size by the end of the activity season. Indeed, such counter-gradient variation in growth rate has been shown in several lizard species (Ferguson and Talent 1993; Sears 2005). Thus, geographic patterns of age and size at maturity will reflect the relative magnitude of these costs and benefits in relation to the length of activity season.

We show that, across their distribution, common lizards in populations with short activity season are larger on average than lizards in populations with long activity seasons. Furthermore, females with short activity periods attain larger minimum body size at maturity (Fig. 3). As growth slows down with the onset of maturity, larger minimum body size can be explained by faster juvenile growth or/and delaying sexual maturation. Our data suggest that the latter is true as females experiencing shorter activity season tend to mature at an older age (not tested due to small sample size, but see data in Table S1). These differences in size and age at first reproduction are consistent with previous studies of reptile and amphibian populations living in different thermal environments, with females generally being larger and maturing later in slow-growth environments (Dunham 1982; Morrison and Hero 2003; Arribas and Galán 2005). Data on age-specific body size in the common lizard suggest that maturation is related to reaching a minimum body size rather than a specific age. However, the threshold clearly differs among populations. For example, females from lowland populations in France (Louvie and Paimpont) may start to reproduce at 1 year old if they reached the size of 40 mm whereas females

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Table 1. Models including geographic predictors.

		Parameter									
		(A) Spatial-phylogenetic models					(B) Models with no correction				
Dependent variable	Predictor	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance
SVL mean	Altitude	0.3029	1.3084	−2.2616	2.8674	0.2224	−0.1560	1.5332	−3.1611	2.8490	0.2604
	Latitude	−0.2625	1.4403	−3.0855	2.5605	0.2141	0.9206	1.5126	−2.0440	3.8852	0.2944
	Length of activity season	−3.9531	0.9852	−5.8841	−2.0221	**1.0000**	−3.8482	1.0184	−5.8442	−1.8521	**0.9940**
	Temperature during activity season	1.0341	1.1104	−1.1422	3.2104	0.3496	0.4529	1.0975	−1.6981	2.6040	0.2567
	Precipitation during activity season	1.6323	0.9173	−0.1655	3.4301	0.6601	1.1503	1.0010	−0.8116	3.1123	0.3817
	Reproductive mode	1.3375	1.1421	−0.9009	3.5759	0.4023	1.5537	1.1714	−0.7423	3.8497	0.4407
SVL min	Altitude	2.6472	2.5650	−2.3801	7.6745	0.3733	2.7467	3.0704	−3.2712	8.7646	0.3427
	Latitude	−0.3479	3.1511	−6.5239	5.8281	0.2186	1.4982	3.3884	−5.1430	8.1394	0.2833
	Length of activity season	−3.4622	1.7408	−6.8740	−0.0503	**0.8778**	−3.4859	1.6694	−6.7578	−0.2140	**0.7284**
	Temperature during activity season	1.0318	2.1515	−3.1851	5.2486	0.1561	0.5804	2.0232	−3.3849	4.5458	0.2436
	Precipitation during activity season	3.1273	1.4944	0.1983	6.0563	**0.8887**	2.8906	1.6003	−0.2459	6.0271	0.6160
	Reproductive mode	−0.0987	2.3474	−4.6995	4.5022	0.2259	0.2491	2.2146	−4.0914	4.5896	0.2359
SVL max	Altitude	−0.3897	2.4381	−5.1684	4.3889	0.2790	0.8957	3.1635	−5.3045	7.0960	0.3328
	Latitude	2.6132	2.5756	−2.4349	7.6614	0.3693	4.3796	2.1392	0.1869	8.5722	**0.7795**
	Length of activity season	−2.3378	1.8838	−6.0300	1.3544	**0.8761**	−2.2461	1.5738	−5.3307	0.8385	0.4695
	Temperature during activity season	0.2084	1.6080	−2.9433	3.3601	0.2124	0.0426	1.7067	−3.3024	3.3877	0.2344
	Precipitation during activity season	2.8391	1.3663	0.1613	5.5169	**0.6946**	2.4878	1.3958	−0.2478	5.2235	0.6049
	Reproductive mode	0.8012	3.9105	−6.8631	8.4656	0.2493	1.8079	2.1917	−2.4877	6.1036	0.3181
Fecundity mean	Altitude	−0.5389	0.5215	−1.5611	0.4832	0.3591	−0.1206	0.5472	−1.1932	0.9519	0.2352
	Latitude	−0.2137	0.6434	−1.4748	1.0474	0.2626	−0.4673	0.5012	−1.4497	0.5151	0.3228
	Length of activity season	0.6011	0.3408	−0.0668	1.2691	0.5913	0.1447	0.3747	−0.5897	0.8791	0.2357
	Temperature during activity season	−0.3921	0.3566	−1.0911	0.3069	0.3517	−0.1498	0.3784	−0.8914	0.5918	0.2314
	Precipitation during activity season	0.2739	0.3031	−0.3202	0.8690	0.2913	0.5788	0.3345	−0.0768	1.2345	0.5780
	Reproductive mode	1.3463	0.3629	0.6350	2.0577	**0.9921**	1.4469	0.4049	0.6532	2.2405	**0.9946**
	Mean SVL	1.4233	0.3746	0.6891	2.1574	**0.9978**	0.8824	0.3423	0.2116	1.5533	**0.8995**
SVL-fecundity slope	Altitude	0.0230	0.0939	−0.1611	0.2071	0.2263	0.0194	0.0950	−0.1667	0.2055	0.2285
	Latitude	−0.1700	0.0571	−0.2820	−0.0580	**0.9255**	−0.1676	0.0561	−0.2776	−0.0576	**0.9213**
	Length of activity season	0.0585	0.0775	−0.0935	0.2104	0.2510	0.0590	0.0701	−0.0784	0.1965	0.2660
	Temperature during activity season	−0.0668	0.0620	−0.1884	0.0548	0.3139	−0.0677	0.0580	−0.1814	0.0460	0.3419
	Precipitation during activity season	−0.0132	0.0537	−0.1185	0.0921	0.1797	−0.0294	0.0546	−0.1346	0.0776	0.2070
	Reproductive mode	0.2073	0.0563	0.0969	0.3177	**0.9984**	0.2138	0.0572	0.1017	0.3258	**0.9898**

Summary of standardized parameter estimates for models of mean, minimum, maximum body size (SVL), mean fecundity (tested also for the effect of mean SVL) and body size-fecundity slope in the studied common lizard (*Zootoca vivipara*) populations, with the following predictors: altitude, latitude, length of activity season, average temperature, and precipitation during the activity season, and reproductive mode. Results are given for (A) models controlling for phylogenetic and spatial autocorrelation and (B) models without spatial or phylogenetic correction. A list of the AIC_c ranks of different models and full details for the top models are presented in Table S2. Parameter importance was calculated as the sum of Akaike weights of all models that include the parameter of interest. In bold are the importance values for those predictors whose 95% confidence intervals exclude zero. SE, standard error; CL, confidence limit of 95% confidence interval.

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Table 2. Models without geographic predictors.

		Parameter									
		(A) Spatial- phylogenetic models					(B) Models with no correction				
Dependent variable	Predictor	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance
SVL mean	Length of activity season	−3.9520	0.9637	−5.8407	−2.0632	**1.0000**	−3.9146	0.9790	−5.8335	−1.9958	**0.9982**
	Temperature during activity season	0.9762	1.0750	−1.1308	3.0832	0.3487	0.4686	1.0596	−1.6082	2.5454	0.2654
	Precipitation during activity season	1.6295	0.9100	−0.1540	3.4130	0.6520	1.0536	0.9781	−0.8635	2.9706	0.3642
	Reproductive mode	1.1771	1.0368	−0.8550	3.2092	0.3915	1.5839	1.0582	−0.4900	3.6579	0.5001
SVL min	Length of activity season	−3.6033	1.6027	−6.7446	−0.4620	**0.9860**	−3.5662	1.5889	−6.6803	−0.4520	**0.7962**
	Temperature during activity season	0.2130	1.7172	−3.1528	3.5787	0.1902	−0.0184	1.6527	−3.2577	3.2210	0.2284
	Precipitation during activity season	3.2543	1.4719	0.3694	6.1392	0.8655	2.9301	1.5780	−0.1627	6.0230	0.6407
	Reproductive mode	−0.7483	1.8058	−4.2875	2.7909	0.2052	−0.2285	1.7832	−3.7234	3.2665	0.2341
SVL max	Length of activity season	−2.2390	1.7698	−5.7078	1.2297	0.8344	−2.5874	1.4881	−5.5041	0.3292	0.5932
	Temperature during activity season	0.1204	1.5417	−2.9013	3.1420	0.2033	−0.4091	1.5774	−3.5009	2.6826	0.2433
	Precipitation during activity season	2.8699	1.3760	0.1730	5.5668	**0.5733**	1.8924	1.4131	−0.8773	4.6620	0.4316
	Reproductive mode	1.0149	3.8939	−6.6169	8.6468	0.2839	3.2870	1.5427	0.2633	6.3107	**0.7557**
Fecundity mean	Length of activity season	0.5890	0.3265	−0.0510	1.2290	0.6116	0.1772	0.3606	−0.5296	0.8840	0.2486
	Temperature during activity season	−0.2838	0.3225	−0.9158	0.3482	0.2973	−0.1248	0.3631	−0.8364	0.5868	0.2321
	Precipitation during activity season	0.2742	0.3000	−0.3138	0.8622	0.3001	0.5985	0.3270	−0.0425	1.2395	0.6269
	Reproductive mode	1.3931	0.3347	0.7371	2.0491	**0.9971**	1.3795	0.3700	0.6542	2.1047	**0.9957**
	Mean SVL	1.3888	0.3688	0.6661	2.1115	**0.9973**	0.8622	0.3401	0.1956	1.5288	**0.8898**
SVL-fecundity slope	Length of activity season	0.1218	0.0804	−0.0356	0.2793	0.7893	0.0971	0.0721	−0.0442	0.2384	0.4453
	Temperature during activity season	−0.1269	0.0747	−0.2733	0.0196	0.6024	−0.0811	0.0776	−0.2333	0.0710	0.3435
	Precipitation during activity season	0.0358	0.0614	−0.0844	0.1561	0.2549	0.0392	0.0573	−0.0730	0.1515	0.2434
	Reproductive mode	0.1415	0.0624	0.0193	0.2637	**0.8933**	0.1323	0.0593	0.0160	0.2486	**0.7628**

Summary of parameter estimates for models of mean, minimum, maximum body size (SVL), mean fecundity (tested also for the effect of mean SVL), and body size-fecundity slope in the studied common lizard (*Zootoca vivipara*) populations, with the following predictors: length of activity season, average temperature and precipitation during the activity season, and reproductive mode. In bold are the importance values for those predictors whose 95% confidence intervals exclude zero. For further explanation see Table 1.

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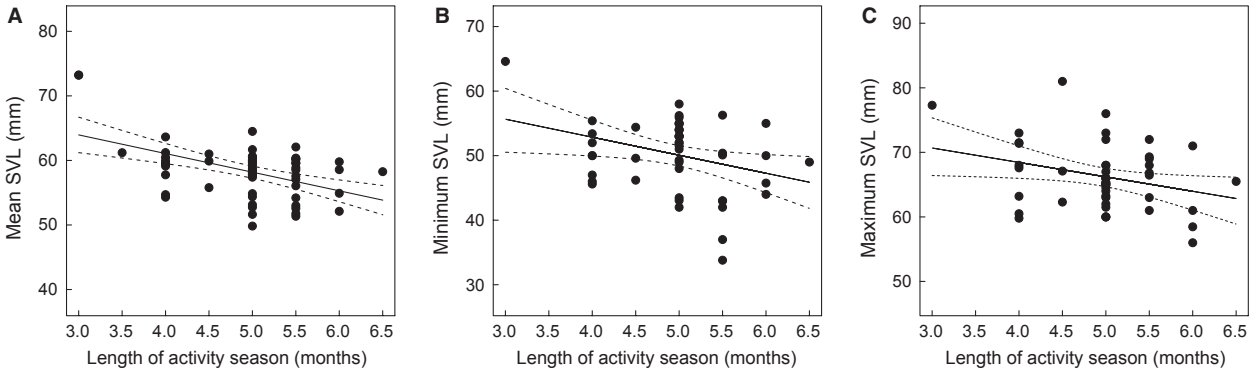

Figure 3. The relationship between body size (SVL) and the length of activity season in studied populations of reproducing female common lizards (*Zootoca vivipara*): (A) mean body size; (B) minimum body size; (C) maximum body size. Dashed lines demarcate the 95% confidence interval.

from populations in Russia, Finland, highland France or Switzerland generally postpone reproduction to the age of 2 or 3 years at the body size of 50–55 mm (Tuula A. Oksanen and Martti Niskanen, unpubl. data; Cavin 1993; Bauwens et al. 1986; Bulakhova et al. 2007). This delayed maturation is not simply caused by the inability to reach the required threshold in a particular year because females larger than 40 mm at emergence of hibernation do not reproduce in some populations with short activity seasons (e.g. Bulakhova et al. 2007). Instead, postponing reproduction to a larger body size may actually confer an advantage in time-constrained environments.

What can this benefit be? Life-history theory predicts that delayed maturation at a larger size is favored in environments where the increment in fecundity or survivorship is relatively high (Roff 1992; Kozlowski et al. 2004; Arendt 2011). If the body size-fecundity relationship is not fixed among populations, one would expect a larger optimal body size in populations where the fecundity increases more rapidly with body size (Arendt 2011). Several different mechanisms can generate variation in the body size-fecundity relationship, such as variation in food availability or predation pressure, both of which may be correlated with seasonal activity patterns (Weetman and Atkinson 2004). However, we found only weak relationship between body size-fecundity relationship and the length of activity season, although the effects were stronger when excluding geographic predictors, suggesting that it may contribute to explaining why lizards mature at a larger size in time-constrained environments.

Another, not mutually exclusive, explanation is that short activity season correlates with other ecological variables that select for delayed maturation and large body size. For example, although lizards with a long activity season may benefit from a greater opportunity for growth, a high frequency of activity is associated with higher risk of predation (e.g. Werner and Anholt 1993), which translates into lower annual survival. Population estimates of survival rates of the common lizard do indeed show that adult survival tends to be higher in populations with shorter activity period (Bauwens et al. 1986; Cavin 1993; Sorci et al. 1996; Heulin et al. 1997). Selection favors early maturation at a smaller size and high reproductive effort in environments with high mortality rates (Roff 1992; Adolph and Porter 1993; Kozlowski et al. 2004). Because low mortality is associated with higher life expectancy, females in low mortality environments can afford to postpone their reproduction and benefit from greater fecundity as a result of reaching larger body size.

Reproductive mode also explained variation in maximum body size, with common lizards in viviparous populations attaining relatively larger body size in comparison to lizards in oviparous populations (Table S1). The largest portion of the female body size is formed by the trunk with abdominal cavity and this is positively selected by fecundity selection to provide enough space for the eggs or developing embryos (Kratochvíl et al. 2003). The larger body size of the viviparous females might be thus the result of the space requirements for the embryos, which develop longer inside the female body than do the eggs of oviparous females (e.g. mass per progeny in viviparous and oviparous females equalled to 0.509 g and 0.264 g, respectively, in skink *Lerista bougainvillii*; Qualls and Shine 1995).

Interpopulation variation in fecundity was mainly explained by the body size and reproductive mode. The positive correlation between body size and clutch size is a common trend for viviparous populations of the common lizard (Avery 1975; Bauwens and Verheyen 1987; Liu et al. 2008; Horváthová et al. 2013), whereas data for oviparous population are rather limited (Braña 1986; Roig et al.

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2000; Lindtke et al. 2010). Lizards in viviparous populations had relatively larger clutch size for their body size than lizards in oviparous populations. One potential explanation is that if oviparous females are able to lay multiple clutches in one breeding season, they may be selected to decrease their investment in each reproductive attempt. This is supported by the fact that the length of gestation is considerably shorter in oviparous than in viviparous populations (14–30 vs. 60–70 days; Heulin 1988; Heulin et al. 1991). Oviparous common lizards from low and moderate altitudes (population Louvie and Gabas) may lay two to three clutches and the total fecundity is comparable to, or higher than, that of lizards in viviparous populations (Heulin et al. 1997). However, most oviparous populations included in this study are from high altitudes experiencing shorter activity period and their reproductive cycle has not been studied in natural conditions. It is therefore difficult to assess to what extent lower clutch size in oviparous populations is generally associated with lower lifetime reproductive output. The other potential explanation is that lower fecundity is traded off by an increased egg/offspring size. Although there is some evidence showing that oviparous females produce larger offspring (Heulin 1988; Lindtke et al. 2010), the data are not sufficient to confirm this hypothesis.

All life-history traits analyzed in this study showed significant spatial autocorrelation suggesting that populations closer to each other were affected more similarly by the same environmental conditions than those separated by larger geographic distance. The effect of geographic distance on body size is usually smaller in taxa that grow continuously throughout their life span (albeit at a reduced rate), such as reptiles, compared to those with more fixed body size, such as mammals and birds (Jetz et al. 2009). However, the large geographic distribution covered by the common lizard makes genetic divergence more likely, which could contribute to the strong spatial effects in our analyses. In contrast to spatial autocorrelation, we found almost no phylogenetic signal explaining variation in life-history traits, which is in concordance with previously reported data on another lizard, *Sceloporus undulatus* (Niewiarowski et al. 2004). However, it is worth noticing that the resolution of the spatial autocorrelation is higher than that of our phylogeny, which to some extent reduces our ability to tease apart evolutionary history and geographic effects.

In summary, we have shown that geographic variation in body size in the common lizards is better explained by differences in the length of activity season than by temperature per se. The common lizard does not exhibit the patterns consistent with Bergmann's clines. We suggest that species with geographically widespread populations will likely exhibit among-population variation in growth and survival as a result of their different activity patterns, which may promote different life-history strategies. Geographic variation in fecundity is mainly explained by differences in average body size of the females as well as reproductive mode (oviparity vs. viviparity), with little evidence for an effect of climate (see also Bleu et al. 2011). Further studies are required to test whether these patterns reflect local adaptation or if the extraordinarily wide geographic and climatic range of the common lizard has been facilitated by an inherent, potentially adaptive, plasticity in life-history traits.

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Environmental and life-history data for the populations of *Zootoca vivipara* included in the comparative analyses.

Table S2. Summaries for phylogenetic-spatial and no-correction models with their parameter estimates.

Appendix: Table A1. The localities and haplotypes of the common lizard (*Zootoca vivipara*) populations and sources of the data used in this study.

Locality no.	Country/Locality	Coordinates (N/E; decimal)	Altitude (m above sea level)	Clade/Haplotype	Source (see references below)
	Spain				
1	Xistral	43.47/−7.54	770	B1/OC4	This study
2	Asturias	43.12/−5.23	1490	B1/OC3-4	Braña (1986)
3	Refugio Andara	43.22/−4.72	1535	B1/OC4	This study
4	Cantabrian Mts.	43.00/−4.00	1500	B1/OC3-4	Arribas (2009)
5	Basque Country	42.00/−1.50	1930	B1/OC1-3	Arribas (2009)
6	Puerto de Ibañeta	43.02/−1.32	1094	B1/OC1	This study
7	Hecho LaMina	42.85/−0.67	1306	B1/OC1	This study
8	Candanchu Censo	42.78/−0.55	1632	B1/OC1	This study
9	Somport Censo	42.79/−0.53	1639	B1/OC1	This study
10	Somport	42.79/−0.53	1631	B1/OC1	This study
11	Formigal Curva	42.80/−0.41	1719	B1/OC1	This study
12	Brocuso	42.80/−0.40	1774	B1/OC1	This study
13	Formigal Turbera	42.80/−0.40	1755	B1/OC1	This study
14	Pyrenées	42.00/0.50	2090	B2/OF1-4	Arribas (2009)
15	Pla de Beret	42.71/0.94	1800	B2/OF1	Roig et al. (2000), Sanchis et al. (2000)
	France				
16	Paimpont	48.00/−2.17	150	E/VB1	Pilorge et al. (1983); Heulin (1985a,b); Arrayago et al. (1996); Stewart et al. (2009)
17	Artxilondo	43.04/−1.13	982	B2/OF1-4	This study
18	Gabas	42.90/−0.42	1100	B1/OC1	Heulin et al. (1994)
19	Louvie	43.09/−0.38	380	B2/OF1	Heulin et al. (1994); Guillaume et al. (2006); Stewart et al. (2009)
20	Lac Montcineyre	45.46/2.90	1100	E/VB1	Pilorge and Xavier (1981), Pilorge et al. (1983)

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Appendix: Table A1. Continued.

Locality no.	Country/Locality	Coordinates (N/E; decimal)	Altitude (m above sea level)	Clade/Haplotype	Source (see references below)
21	Lac Pavin	45.50/2.91	1200	E/VB1	Pilorge and Xavier (1981); Pilorge (1982); Pilorge et al. (1983)
22	Col de la Moréno	45.73/2.93	1000	E/VB1	Pilorge and Xavier (1981); Pilorge et al. (1983)
23	Le Chalet du Mont Lozère	44.48/3.72	1410	E/VB1	Pilorge (1987)
24	Mas de la Barque	44.38/3.82	1425	E/VB1	Pilorge (1987)
25	Plateau de la Croix de l'Ermite	44.38/3.89	1465	E/VB1	Pilorge (1987)
	Great Britain				
26	Priddy	51.25/−2.66	210	E/VB1	Avery (1975)
	Belgium				
27	Kalmthoutse Heide	51.41/4.41	50	E/VB1	Pilorge et al. (1983); Bauwens and Verheyen (1987); Van Damme et al. (1989)
	Netherlands				
28	De Hamert	51.53/6.17	115	E/VB1	Strijbosch and Creemers (1988)
	Germany				
29	Oberdrees	50.63/6.91	170	E/VB1	Kornacker (1993)
30	Leipzig	51.36/12.23	95	E/VB1	Hofmann and Henle (2006)
	Switzerland				
31	Berne Foralps	46.58/7.66	1500	E/VB1	Cavin (1993)
	Austria				
32	Carinthia	46.58/13.13	1480	E/VB11	Lindtke et al. (2010)
33	Carinthia	46.60/13.13	1430	A/OS10	Lindtke et al. (2010)
	Poland				
34	Odolanów	51.57/17.66	140	E/VB1	Ekner et al. (2008)
	Slovakia				
35	Žiar	49.13/19.66	830	E/VB12-14	This study; Horváthová et al. (2013)
36	Šuňava	49.01/20.11	875	E/VB12-14	This study; Horváthová et al. (2013)
	Bosnia and Herzegevina				
37	Mountain Vlašić	44.28/17.63	1850	E/VB11	This study
38	Sara Mt.	41.83/20.67	2200	E/VB11	Crnobrnja-Isailović and Aleksić (2004)
39	Stara Mt.	43.37/22.75	1880	E/VB11	Crnobrnja-Isailović and Aleksić (2004)
	Romania				
40	Sureanu Mts.	45.60/23.30	810	D/VU9	This study
	Bulgaria				
41	Bulgarian Mts.	41.00/23.00	1640	E/VB11-14	Guillaume et al. (1997)
	Sweden				
42	Asketunnan, Hållsundsudde	57.36/11.96	10	E/VB1	This study
43	Sandsjöbacka	57.53/12.03	100	E/VB1	This study
44	Öjersjö	57.70/12.13	120	E/VB1	This study
45	Markitta	67.16/21.50	300	D/VU1	This study
	Finland				
46	Helsinki	60.17/24.88	0	D/VU1	This study
47	Jyväskylä 2	62.18/25.33	155	D/VU1	This study
48	Jyväskylä 1	62.10/25.45	139	D/VU1	This study
49	Petäjävesi	62.17/25.70	120	D/VU1	This study
50	Oulanka	66.37/29.32	200	D/VU1	This study
	Russia				
51	Moscow	55.75/37.58	200	D/VU2	Guillaume et al. (2006)
52	Pershino	57.28/84.17	60	D/VU1	Bulakhova et al. (2007)
53	Russian taiga zone	53.50/84.83	270	D/VU1	Saveliev et al. (2006)
54	Timiryazevskiy village	56.47/84.90	100	D/VU1	Bulakhova et al. (2007)
55	Tomsk	56.50/84.96	125	D/VU1	Orlova et al. (2005)
56	Kebezen	51.91/87.10	475	D/VU1	Orlova et al. (2005); Bulakhova et al. (2007)
57	Gavrilovka	56.63/88.10	550	D/VU1	Bulakhova et al. (2007)
58	Prichulym'e	57.30/88.20	350	D/VU1	Orlova et al. (2005)

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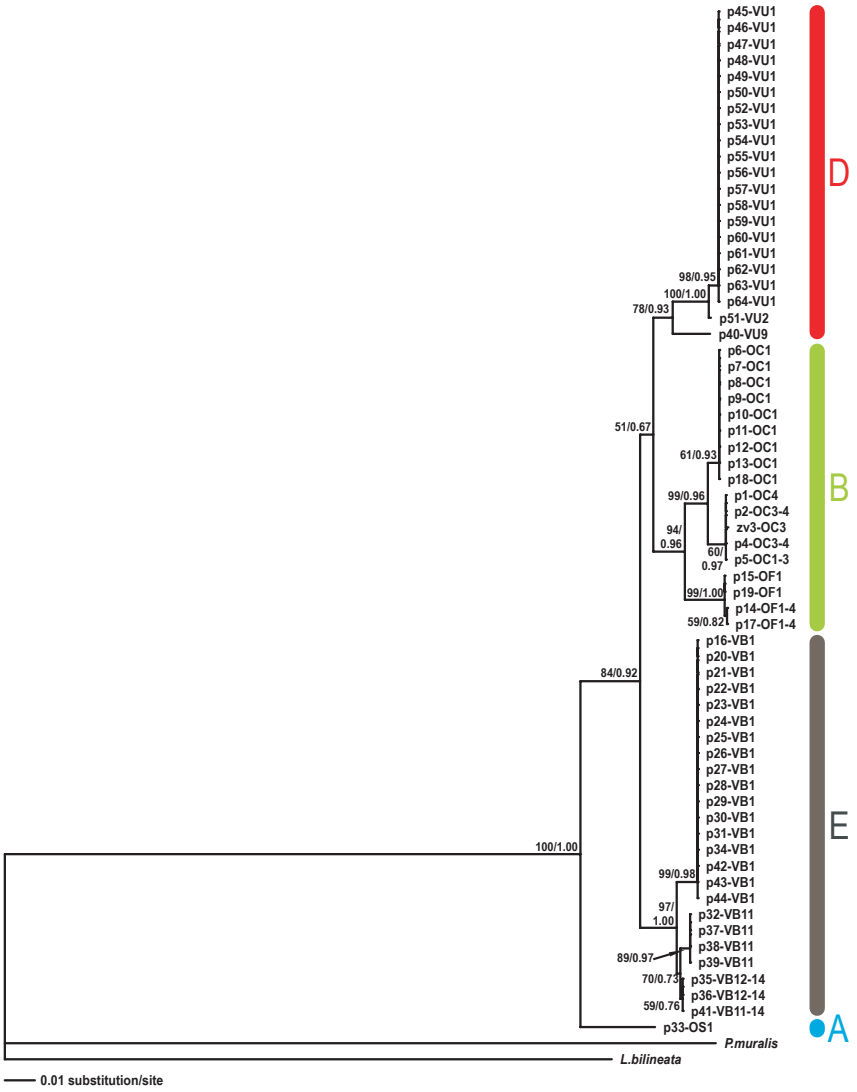
Appendix: Table A1. Continued.

Locality no.	Country/Locality	Coordinates (N/E; decimal)	Altitude (m above sea level)	Clade/Haplotype	Source (see references below)
59	Khakassiya Republic	54.63/88.62	1170	D/VU1	Bulakhova et al. (2007)
60	Chudnoe Lake	54.13/88.75	1170	D/VU1	Orlova et al. (2005)
61	Komsomolskiy Nature Reserve	50.56/137.00	500	D/VU1	Lazareva (2009)
	Kazakhstan				
62	Uspenka	49.23/85.75	1500	D/VU1	Orlova et al. (2005)
63	Urunhaika	48.76/86.00	1550	D/VU1	Orlova et al. (2005)
	China				
64	Sunwu County	49.65/127.57	304	D/VU1	Liu et al. (2008)

Appendix: Figure A1.

Maximum likelihood phylogeny of the common lizard populations used in this study. The population numbers correspond to those in Fig. 2 and Table A1 and are accompanied by the haplotype name(s) associated with the particular populations. The statistical support of the branches is expressed as percentage bootstrap values/SH-like aLRT probabilities.



Appendix: Table A2. Variance inflation factors for all model sets, (A) for models with viviparous and oviparous populations, (B) for models with viviparous populations.

(A)	Spatial-phylogenetic models with all predictors				
Predictor/Dependent variable	SVL mean	SVL min	SVL max	Fecundity mean	SVL-fecundity slope
Altitude	4.8942	6.4302	4.2260	4.5628	5.0460
Latitude	5.1127	6.0559	2.2998	4.7885	5.2462
Length of activity season	1.7267	1.9101	1.9052	1.9569	3.8131
Temperature during activity season	1.8011	2.0724	1.8803	1.7344	2.8210
Precipitation during activity season	1.2265	1.0874	1.2206	1.3186	1.8974
Reproductive mode	1.6937	2.0466	1.1573	1.5226	1.1992
Mean SVL	–	–	–	1.6346	–
No-correction models with all predictors					
Altitude	5.2618	7.0148	7.0148	5.3186	4.8670
Latitude	5.6715	7.1216	7.1216	5.6546	5.5782
Length of activity season	1.7137	1.9302	1.9302	1.7306	3.3131
Temperature during activity season	1.8767	2.1609	2.1609	1.7654	2.2318
Precipitation during activity season	1.2806	1.1245	1.1245	1.2689	1.8039
Reproductive mode	1.8874	2.2912	2.2912	1.6251	1.3150
Mean SVL	–	–	–	1.3420	
Spatial-phylogenetic models with altitude and latitude excluded					
Length of activity season	1.0790	1.0726	1.0451	1.3790	2.1673
Temperature during activity season	1.3476	1.2127	1.1554	1.3373	2.7908
Precipitation during activity season	1.1826	1.0576	1.1609	1.2945	1.6242
Reproductive mode	1.2038	1.2257	1.0647	1.2068	1.0189
Mean SVL	–	–	–	1.5510	–
No-correction models with altitude and latitude excluded					
Length of activity season	1.0899	1.0972	1.0972	1.2607	2.0352
Temperature during activity season	1.3042	1.1652	1.1652	1.3120	2.2155
Precipitation during activity season	1.1601	1.0413	1.0413	1.1531	1.4023
Reproductive mode	1.2184	1.2288	1.2288	1.2455	1.0237
Mean SVL	–	–	–	1.3279	–

(B)	Spatial-phylogenetic models with all predictors				
Predictor/Dependent variable	SVL mean	SVL min	SVL max	Fecundity mean	SVL-fecundity slope
Altitude	4.4112	4.6051	5.1594	4.5321	6.8181
Latitude	4.3183	2.8542	4.1956	4.5039	6.6314
Length of activity season	1.7411	1.9425	1.9472	2.2047	5.2505
Temperature during activity season	1.6653	1.8175	1.9606	1.7058	4.1067
Precipitation during activity season	1.3247	1.1056	1.1305	1.4878	2.6273
Mean SVL	–	–	–	1.7450	
No-correction models with all predictors					
Altitude	4.6711	5.7481	5.7481	5.0891	6.1280
Latitude	4.6668	5.2220	5.2220	5.2469	6.7544
Length of activity season	1.6930	1.9254	1.9254	1.8290	4.1647
Temperature during activity season	1.6976	2.0733	2.0733	1.6038	2.4202
Precipitation during activity season	1.3052	1.1363	1.1363	1.4096	2.2117
Mean SVL	–	–	–	1.3958	–
Spatial-phylogenetic models with altitude and latitude excluded					
Length of activity season	1.0238	1.0036	1.0036	1.4422	2.3421
Temperature during activity season	1.2125	1.0248	1.0248	1.2664	3.7463
Precipitation during activity season	1.1911	1.0283	1.0283	1.3606	2.0564
Mean SVL	–	–	–	1.5618	–
No-correction models with altitude and latitude excluded					
Length of activity season	1.0126	1.0012	1.0012	1.2873	2.0199
Temperature during activity season	1.0889	1.0009	1.0009	1.1073	2.3565
Precipitation during activity season	1.0883	1.0008	1.0008	1.1487	1.4459
Mean SVL	–	–	–	1.3414	–

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Appendix: Table A3. Models for viviparous populations.

		Parameter									
		(A) Spatial-phylogenetic models					(B) Models with no correction				
Dependent variable	Predictor	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance
SVL mean	Altitude	1.7333	1.4470	−1.1028	4.5693	0.4163	1.4861	1.9393	−2.3149	5.2871	0.2975
	Latitude	−1.2968	1.7881	−4.8013	2.2077	0.3341	0.8247	2.1824	−3.4528	5.1022	0.2514
	Length of activity season	−4.8312	1.2263	−7.2346	−2.4278	**0.9963**	−4.6268	1.2617	−7.0997	−2.1540	**0.9863**
	Temperature during activity season	0.6055	1.3533	−2.0470	3.2580	0.2451	−0.1520	1.3432	−2.7846	2.4805	0.2278
	Precipitation during activity season	1.3657	1.1087	−0.8074	3.5388	0.3875	1.1006	1.2616	−1.3722	3.5733	0.2995
SVL min	Altitude	6.5284	2.5388	1.5523	11.5044	**0.9442**	5.5417	3.6796	−1.6701	12.7535	0.5568
	Latitude	0.0046	3.7900	−7.4237	7.4330	0.2011	4.0174	4.2113	−4.2366	12.2714	0.3747
	Length of activity season	−0.4609	3.7721	−7.8541	6.9323	0.1677	−4.1404	2.3190	−8.6856	0.4048	0.5724
	Temperature during activity season	1.9878	2.4948	−2.9019	6.8776	0.2217	−0.6903	2.8038	−6.1856	4.8051	0.2462
	Precipitation during activity season	3.7708	1.8249	0.1940	7.3476	0.7051	3.6359	2.1684	−0.6140	7.8858	0.5317
SVL max	Altitude	−0.3907	2.6515	−5.5876	4.8062	0.2241	−1.1189	2.8954	−6.7938	4.5560	0.2678
	Latitude	2.1380	2.6716	−3.0982	7.3743	0.2790	3.0109	2.3970	−1.6871	7.7090	0.4091
	Length of activity season	−2.9145	1.9728	−6.7810	0.9521	0.4531	−2.8102	2.0424	−6.8131	1.1928	0.4229
	Temperature during activity season	0.4134	2.2043	−3.9070	4.7337	0.2059	−0.1248	2.1356	−4.3105	4.0610	0.2077
	Precipitation during activity season	2.6457	1.7895	−0.8617	6.1531	0.4512	2.2052	2.1002	−1.9110	6.3215	0.3280
Fecundity mean	Altitude	−1.0989	0.6720	−2.4160	0.2182	0.6827	−1.0626	0.6111	−2.2604	0.1351	0.6180
	Latitude	−0.9363	0.7459	−2.3983	0.5257	0.4789	−1.1951	0.6274	−2.4247	0.0346	0.7209
	Length of activity season	0.8631	0.3835	0.1114	1.6148	**0.7283**	0.3368	0.4235	−0.4932	1.1668	0.2845
	Temperature during activity season	−0.5531	0.3458	−1.2309	0.1247	0.5052	−0.2157	0.3979	−0.9956	0.5643	0.2574
	Precipitation during activity season	0.2309	0.3159	−0.3883	0.8501	0.2453	0.3906	0.3393	−0.2745	1.0557	0.3337
	Mean SVL	2.0562	0.3787	1.3140	2.7984	**1.0000**	1.5552	0.3448	0.8794	2.2311	**0.9994**
SVL-fecundity slope	Altitude	0.0325	0.1055	−0.1743	0.2393	0.2146	0.0528	0.1083	−0.1594	0.2650	0.2402
	Latitude	−0.1837	0.0608	−0.3030	−0.0645	**0.9268**	−0.1777	0.0604	−0.2961	−0.0593	**0.8948**
	Length of activity season	0.0240	0.0857	−0.1441	0.1920	0.2001	0.0491	0.0850	−0.1176	0.2158	0.2269
	Temperature during activity season	−0.0684	0.0666	−0.1989	0.0621	0.2861	−0.0885	0.0655	−0.2169	0.0399	0.4034
	Precipitation during activity season	−0.0239	0.0715	−0.1640	0.1161	0.1844	−0.0629	0.0724	−0.2047	0.0790	0.2607

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Appendix: Table A3. Continued

Models with excluded latitude and altitude

		Parameter									
		(C) Spatial-phylogenetic models					(D) Models with no correction				
Dependent variable	Predictor	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance	Model-averaged β	Unconditional SE	Lower CL	Upper CL	Relative importance
SVL mean	Length of activity season	−4.7668	1.1481	−7.0169	−2.5166	**1.0000**	−4.7204	1.1968	−7.0661	−2.3747	**0.9970**
	Temperature during activity season	0.2244	1.2767	−2.2778	2.7266	0.2331	−0.3307	1.2311	−2.7436	2.0821	0.2328
	Precipitation during activity season	1.5605	1.0662	−0.5292	3.6502	0.4745	1.0995	1.2113	−1.2747	3.4737	0.3117
SVL min	Length of activity season	−4.9398	2.2057	−9.2628	−0.6167	**0.8579**	−4.6482	2.0939	−8.7521	−0.5444	**0.7666**
	Temperature during activity season	−1.3262	2.3572	−5.9462	3.2938	0.2306	−1.8779	2.1341	−6.0607	2.3049	0.2830
	Precipitation during activity season	4.2052	1.9585	0.3665	8.0438	**0.9377**	3.7561	2.0923	−0.3447	7.8569	0.5898
SVL max	Length of activity season	−2.9054	1.9072	−6.6434	0.8327	0.4757	−2.7552	1.9612	−6.5990	1.0886	0.4405
	Temperature during activity season	0.4197	2.0957	−3.6878	4.5271	0.2141	−0.2030	2.0070	−4.1367	3.7307	0.2155
	Precipitation during activity season	2.4615	1.7453	−0.9591	5.8822	0.4280	1.5350	1.9896	−2.3645	5.4344	0.2750
Fecundity mean	Length of activity season	0.8941	0.3372	0.2332	1.5549	**0.8894**	0.5247	0.3457	−0.1529	1.2024	0.4738
	Temperature during activity season	−0.2444	0.3107	−0.8534	0.3646	0.2657	0.0738	0.3319	−0.5767	0.7243	0.2113
	Precipitation during activity season	0.2797	0.2923	−0.2932	0.8526	0.2911	0.4981	0.3194	−0.1279	1.1240	0.4913
	Mean SVL	1.9525	0.3773	1.2131	2.6919	**0.9999**	1.4419	0.3587	0.7388	2.1450	**0.9985**
SVL-fecundity slope	Length of activity season	0.0616	0.0998	−0.1340	0.2571	0.2478	0.0920	0.0822	−0.0691	0.2531	**0.3509**
	Temperature during activity season	−0.0834	0.0846	−0.2491	0.0823	0.2888	−0.0808	0.0880	−0.2533	0.0918	0.3011
	Precipitation during activity season	0.0539	0.0665	−0.0765	0.1843	0.2505	0.0567	0.0650	−0.0706	0.1841	0.2687

Summary of standardized parameter estimates for models of mean, minimum, maximum body size (SVL), mean fecundity (tested also for the effect of mean SVL) and body size-fecundity slope in the studied viviparous populations of common lizard (*Zootoca vivipara*), with the following predictors: altitude, latitude (these two predictors were excluded in C and D), length of activity season, average temperature, and precipitation during the activity season. Results are given for (A, C) models controlling for phylogenetic and spatial autocorrelation and (B, D) models without spatial or phylogenetic correction. A list of the AIC_c ranks of different models and full details for the top models are presented in Table S2. Parameter importance was calculated as the sum of Akaike weights of all models that include the parameter of interest. In bold are the importance values for those predictors whose 95% confidence intervals exclude zero. SE, standard error; CL, confidence limit of 95% confidence interval.

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