

Natural selection on hatchling body size and mass in two environments in the common lizard (*Lacerta vivipara*)

Gabriele Sorci* and Jean Clobert

Laboratoire d'Ecologie, CNRS UMR 7625, Université Pierre et Marie Curie, Bât. A, 7ème étage,
7 quai St. Bernard, case 237, F-75252 Paris Cedex 05, France

ABSTRACT

Differences in life-history traits among populations living in different environments can arise as adaptations to different selective regimes present in these environments. In this study, we investigated patterns of natural selection on body size (snout-vent length and tail length) and mass in hatchlings of the common lizard (*Lacerta vivipara*) raised in two different environments, where the local populations of *L. vivipara* have different life-history traits. To investigate patterns of natural selection, we raised hatchlings from one high-altitude population in outdoor enclosures located at high and low altitude and we recaptured them before they entered hibernation. We found significant directional selection for higher hatchling body mass and tail length at both sites, whereas hatchling snout-vent length was not correlated with survival. Stabilizing selection gradients were not significant for any of the traits considered at both sites. Differential hatchling mortality may directly affect maternal investment in litter size. In this case, the proper focus of selection might be on mothers. We checked this issue by estimating: (1) the trade-off between litter size and hatchling size and mass; and (2) the correlation between litter size and the proportion of living offspring per litter. Although litter size was negatively associated with hatchling size and mass, we did not find any correlation between fecundity and offspring survival. In conclusion, we found no differences in the patterns of selection between the two environments. These findings are in agreement with previous results showing that differences in life-history traits between these high- and low-altitude populations may arise from plastic responses to proximate cues, rather than genetic adaptation to different selection pressures.

Keywords: body mass, body size, environment, *Lacerta vivipara*, natural selection, survival.

INTRODUCTION

Fluctuating selection pressures in time and space may be responsible for several phenomena observed in natural populations of animals and plants (Schluter *et al.*, 1991). Fluctuating selection can, for instance, contribute to the maintenance of genetic variation in fitness-linked traits (Stearns 1992), affect the sign of the genetic correlation matrices of metric

* Author to whom all correspondence should be addressed. e-mail: gsorci@snv.jussieu.fr

traits (Schluter *et al.*, 1991), and favour individuals with average phenotypes (Sinervo *et al.*, 1992).

Another acknowledged phenomenon arising from fluctuating selection in space is adaptation to the local environment. Life-history as well as morphological traits are known to vary for a single species across populations living in different environments (e.g. Berven, 1982; Vøllestad, 1992; Henmi, 1993; Niewiarowski, 1994). This geographic variation has at least two possible adaptive explanations: (1) each environment has its peculiar selective regime and therefore selects for individuals with the appropriate phenotypic characteristics which may differ from those of another environment (i.e. genetic adaptation to the local environment); and (2) organisms that have plastic phenotypes may use some cues provided by the local environmental conditions and adopt the phenotype appropriate to such conditions (adaptation to the local environment through plastic responses). Convincing evidence exists for both of these mechanisms (Ballinger, 1977; Dunham, 1978; Jones *et al.*, 1987; Sinervo and Adolph, 1989, 1994; Grant and Dunham, 1990; Sinervo, 1990; Rawson and Hilbish, 1991; Sorci *et al.*, 1996a).

In reptiles, several environmental factors can account for the phenotypic plasticity of life histories and morphology. A large body of literature (Stamps and Tanaka, 1981; Andrews, 1982; Avery, 1984; Sinervo and Adolph, 1989, 1994; Niewiarowski and Roosenburg, 1993) has helped to demonstrate that variation in life histories among lizard populations can depend largely on thermal environments without necessarily invoking genetic adaptation to these thermal environments (Adolph and Porter, 1993). On the other hand, a few common garden and reciprocal transplant studies have also noted that genetic differences in life-history traits between lizard populations do exist (Ferguson and Brockman, 1980; Sinervo and Adolph, 1989; Ferguson and Talent, 1993; Niewiarowski and Roosenburg, 1993). This suggests that natural selection could have favoured different genotypes in different environments resulting in genetic differentiation among populations.

Lacerta vivipara is a widespread lacertid lizard ranging from northern Spain to the Pacific coast of Russia, and from Scandinavia to southern Romania. Within this wide range, several populations of *L. vivipara* have been studied in western Europe (France: Pilorge, 1982, 1987; Pilorge *et al.*, 1983, 1987; Heulin, 1985a,b; Massot *et al.*, 1992, 1994; Clobert *et al.*, 1994; Sorci *et al.*, 1994, 1995, 1996a,b; Sorci and Clobert, 1995; Belgium: Bauwens and Verheyen, 1985, 1987; Great Britain: Avery, 1975; Netherlands: Strijbosch and Creemers, 1988). These studies have noted that there is a large amount of geographic variation in life-history traits among populations of the common lizard (e.g. Bauwens *et al.*, 1986). At a smaller scale, two French populations, one at low altitude (150 m) in northern France (Brittany) and the other at high altitude (1400 m) in southern France (Lozère), have different associations of life-history traits (Bauwens *et al.*, 1986; Sorci *et al.*, 1996a). Individuals from the low-altitude population have lower juvenile survival, a higher growth rate, they can reach sexual maturity at the age of 1 year, and they have lower adult survival relative to the high-altitude population (Bauwens *et al.*, 1986; Sorci *et al.*, 1996a).

Here, we report the results of a transplant field enclosure experiment on the patterns of natural selection on hatchling body size and mass in the two environments. Our main aim was to investigate if the observed geographic variation in life histories and morphology between the Lozère and Brittany populations of the common lizard can be accounted for by different patterns of selection acting during early ontogeny (between birth and the first hibernation), when mortality costs are supposed to be at their highest. We also investigated

if differential hatchling mortalities may affect optimal maternal investment in reproduction, measured as litter size.

MATERIALS AND METHODS

Study organism and sites

The common lizard is a live-bearing lacertid living in peat bogs and heathland. Adult snout-vent length (SVL) ranges from 50 to 70 mm. Mating takes place in May, with parturition beginning 2 months later. Females lay an average of five (range 1–12) unshelled eggs that hatch immediately after being laid. However, some of the most southern populations of *L. vivipara* (French Pyrenees and Spain) are oviparous, and females lay shelled eggs that hatch several days after being laid (Heulin and Guillaume, 1989; Heulin *et al.*, 1991).

We studied one high-altitude (1400 m) population of *L. vivipara* in southern France (Mont Lozère, Lozère, 44°N). Most of the life-history traits of this population differ from those of a low-altitude population located in Brittany (Paimpont, 48°N) (Bauwens *et al.*, 1986). More detailed information on site description and the life histories of the two populations can be found in Heulin (1985a,b), Bauwens *et al.* (1986), Pilorge (1987), Massot *et al.* (1992, 1994), Clobert *et al.* (1994) and Sorci *et al.* (1996a).

Outdoor enclosure experiment

At the beginning of July 1994, we captured 44 gravid females from the population located at Mont Lozère. Gravid females were measured (snout-vent length) and weighed. Lizards were then housed in plastic terraria (25 × 15 × 17 cm high) with damp soil, a shelter, water and food (larvae of the Lepidoptera *Pyralis farinalis*) *ad libitum*. They were exposed to a natural photoperiod and to incandescent lamps for heat for 6 h each day. The terraria were randomly placed on a shelf and checked twice daily for hatchlings. Each post-partum female was weighed. Hatchlings were measured (snout-vent length, total length), weighed, marked by toe-clipping, and randomly assigned to a terrarium with damp soil and a shelter within 1 day of birth. By the beginning of August, all of the 44 gravid females had laid their eggs. On 8 August, each hatchling was randomly assigned to one of four enclosures (6.20 × 3.60 × 0.80 m high), either in Lozère or Brittany. Each family was split between the two sites (litter size was always >3, which allowed us to have at least two siblings at each site). The subsequent day, hatchlings were released in the enclosures. Hatchlings released in Brittany had the same mean (±S.D.) SVL and mass as those released in Lozère [SVL: Brittany, 23.03 ± 1.13 mm, $n = 44$; Lozère, 22.97 ± 0.99 mm, $n = 44$; one-way ANOVA, $F_{1,86} = 0.09$, $P = 0.764$; mass: Brittany, 0.198 ± 0.021 g, $n = 44$; Lozère, 0.198 ± 0.021 g, $n = 44$, one-way ANOVA, $F_{1,86} = 0.01$, $P = 0.906$]. The enclosures were located near the natural populations, contained the types of vegetation represented in the natural sites (i.e. grassland vs heathland and peatbogs), and were cleared of all native lizards. Three of the four enclosures contained 30 unrelated hatchlings, whereas the last one contained 29 hatchlings. Because of this relatively high density – natural adult densities in the two sites range from 200 to 300 individuals per hectare in Brittany and from 700 to 1300 individuals per hectare in Lozère (Sorci *et al.*, 1996a) – we added ±400 one-week-old crickets to each enclosure 3 days after the hatchlings were released. The aim of this was to reduce any possible difference in food resources between sites. Between 7 and 10 September – that is, a

few days before hibernation began – we recaptured surviving lizards over three consecutive days. Each lizard was measured, weighed and returned to the enclosure.

Statistical analyses

We assumed that all lizards not recaptured were dead. To test this assumption, we used the program SURGE4 (Pradel *et al.*, 1990) to estimate recapture rates (p_i). Overall cumulative recapture rates (P) were calculated as:

$$P = p_1 + (1 - p_1)p_2 + (1 - p_1)(1 - p_2)p_3$$

where p_1 , p_2 and p_3 represent the recapture rates on the first, second and third days of capture respectively. Overall cumulative recapture rates were high and close to 1 at both sites (Brittany, $P = 0.997$; Lozère, $P = 0.987$), supporting our assumption. As previously noted, we built four enclosures at each site to allow for replicates. As neither survival nor growth rates differed among enclosures within sites (all $P > 0.5$), we pooled the data for each site.

Surviving hatchlings were assigned a fitness value of 1 and non-surviving hatchlings a value of 0. Relative fitness (w) was the individual fitness divided by the mean fitness of all individuals at each site (Brodie *et al.*, 1995). We considered three morphological characters: snout-vent length, body mass and tail length (measured as the difference between total length and snout-vent length). These three traits were correlated among individuals at Lozère (Pearson's correlation coefficient, mass *vs* SVL: $r = 0.520$, $P < 0.001$; mass *vs* tail length: $r = 0.621$, $P < 0.001$; SVL *vs* tail length: $r = 0.208$, $P = 0.024$), whereas SVL and tail length were not correlated among individuals transplanted in Brittany (mass *vs* SVL: $r = 0.311$, $P < 0.001$; mass *vs* tail length: $r = 0.526$, $P < 0.001$; SVL *vs* tail length: $r = -0.067$, $P = 0.472$). Each trait was standardized with mean = 0 and variance = 1 (proc STANDARD, SAS Institute, 1992).

Standardized directional selection differentials (s) were estimated as the slope of the univariate regression of w on the standardized trait (proc REG, SAS Institute, 1992) (Lindén *et al.*, 1992). The significance of s was tested using three methods: (1) comparing mean values of each trait in surviving and non-surviving individuals by t -tests (proc TTEST, SAS Institute, 1992); (2) using logistic regression analysis (proc LOGISTIC, SAS Institute, 1992); (3) using a randomization test (Sokal and Rohlf, 1981; Jayne and Bennett, 1990). This randomization test was performed as follows: We drew random subsamples (each with n = number of observed survivors) from the initial sample containing both the surviving and non-surviving individuals. The mean of each character was determined for these random subsamples and compared to the means observed for the actual survivors. We used 1000 samples to estimate the probability of a randomly drawn subsample having higher mean values than that observed for the survivors (one-tailed test).

Standardized stabilizing selection differentials (c) were estimated as the slope of a multivariate regression of w on the standardized trait (linear and z -transformed squared terms) (Lindén *et al.*, 1992). The significance of c was tested using the randomization test described above with the difference that we compared the variance of each trait in random subsamples to the observed variance of each trait for the survivors (Jayne and Bennett, 1990). As for directional selection, we also used a logistic regression analysis to test significance of stabilizing selection differentials.

Finally, a cubic spline function (Schluter, 1988) was used to estimate the fitness function of each trait in each environment.

Hatchlings sharing the same gene pool may have similar survival probabilities and morphologies when compared to non-sibs. We previously reported a family effect on survival and on body size in the common lizard (Sorci *et al.*, 1994, 1996a). Using each hatchling as an independent point in the logistic regression analysis may thus inflate degrees of freedom and bias the *P*-values. To take account of this, we performed two supplementary analyses. In the first, we computed the family mean of each morphological trait and we correlated (Spearman's correlation coefficient) these values with the percentage of surviving hatchlings per family. This was done for both sites (low and high altitude). The sample size was thus reduced to the number of different families. In the second analysis, we addressed the issue of selection within families. We restricted the analysis to those families including both survivors and non-survivors and we compared, using a binomial test, the body size, mass and tail length of surviving and non-surviving sibs. This was also done for both sites.

To compare patterns of selection between sites, we used a log-linear model (proc CATMOD, SAS Institute, 1992), where survival was a function of the morphological traits, the site and their interactions. A significant interaction between the morphological traits and the site would indicate a difference in selection pressures between sites.

RESULTS

Selection on hatchlings

Hatchling lizards from the Lozère population had higher survival in Lozère than in Brittany (63% or 75/119 vs 23% or 27/119; $\chi^2_1 = 16.133$, $P < 0.001$). Table 1 reports the mean and standard deviation of each morphological trait for survivors and non-survivors at the two sites. The directional differential analyses showed that hatchling body mass and tail length of survivors were higher than those of non-survivors at both sites (Table 2; Figs 1 and 2). Conversely, hatchling snout-vent length did not differ significantly between survivors and non-survivors in Lozère and in Brittany (Table 2, Fig. 3). The stabilizing differential analyses did not provide any evidence of stabilizing selection on any of the three morphological traits, either at the high-altitude or at the low-altitude site (Table 3). The cubic spline estimate of the fitness function (Schluter, 1988) was in line with the results of the selection differentials, since the fitness functions did not suggest any mode, except for hatchling snout-vent length in Brittany (Figs 4–6).

Including all the morphological traits in a multiple stepwise logistic regression model, as both linear and *z*-transformed squared terms, we found that hatchling body mass was the

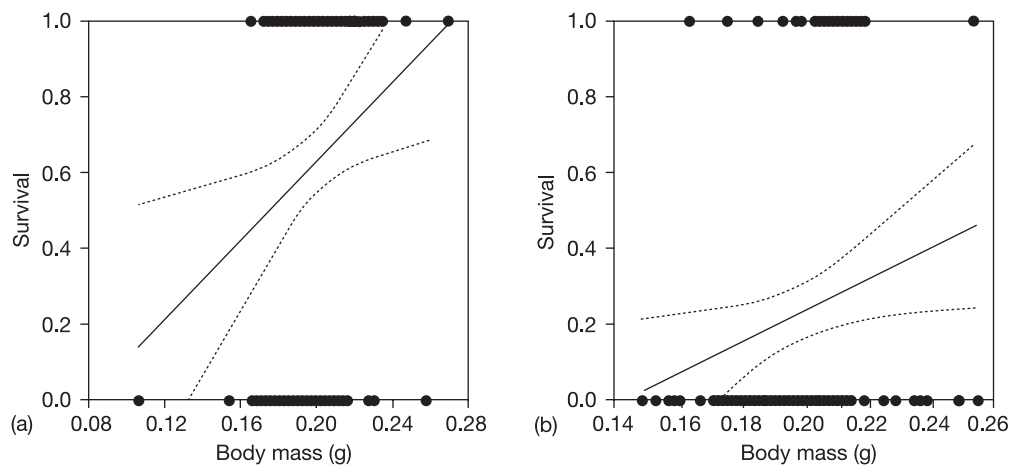
Table 1. Mean $\pm$ standard deviation and sample size (in parentheses) for body mass, snout-vent length and tail length for survivors and non-survivors at the two sites (Lozère and Brittany)

	Brittany		Lozère	
	Survivors	Non-survivors	Survivors	Non-survivors
Body mass (g)	0.205 $\pm$ 0.016 (27)	0.195 $\pm$ 0.022 (92)	0.203 $\pm$ 0.019 (75)	0.192 $\pm$ 0.024 (44)
Snout-vent length (mm)	23.26 $\pm$ 1.13 (27)	22.86 $\pm$ 1.26 (92)	23.05 $\pm$ 1.13 (75)	22.84 $\pm$ 1.10 (44)
Tail length (mm)	24.52 $\pm$ 1.55 (27)	23.41 $\pm$ 1.86 (92)	24.11 $\pm$ 1.68 (75)	23.25 $\pm$ 2.52 (44)

Table 2. Standardized directional differentials (s) and their significance (P) for body mass, snout-vent length and tail length at the two sites (Lozère and Brittany)

	Brittany				Lozère			
	s	P^a	P^b	P^c	s	P^a	P^b	P^c
Body mass	0.137	0.025	0.004	0.028	0.182	0.010	0.042	0.014
Snout-vent length	0.091	0.141	0.073	0.142	0.071	0.318	0.299	0.317
Tail length	0.168	0.006	0.004	0.007	0.155	0.028	0.071	0.037

^a Significance by t -tests comparing the mean value of survivors and non-survivors. ^b Significance by randomization tests (see Methods). ^c Significance by logistic regression.

**Fig. 1.** Relationship between survival and body mass in Lozère (a) and Brittany (b). Dots at 1 and 0 respectively indicate surviving and non-surviving hatchlings. The solid line represents a linear regression line fitted to the points, the dotted lines the 95% confidence intervals of the regression line.

only significant predictor of survival in Lozère ($\chi^2_1 = 6.046$, $P = 0.014$), whereas hatchling tail length was the only significant predictor of survival in Brittany ($\chi^2_1 = 7.234$, $P = 0.007$).

The analyses on family means and within families provided similar results, suggesting that considering each hatchling as an independent observation did not significantly bias the results. We found: (1) positive and significant correlations between percentage of surviving sibs per litter and litter mean body mass at both sites (Brittany: Spearman's $r = 0.434$, $P = 0.004$, $n = 44$; Lozère, Spearman's $r = 0.433$, $P = 0.004$, $n = 44$); (2) a positive correlation between survival and tail length (although not significant in Lozère) (Brittany: Spearman's $r = 0.341$, $P = 0.025$, $n = 44$; Lozère, Spearman's $r = 0.217$, $P = 0.157$, $n = 44$); and (3) a non-significant correlation between survival and SVL at both sites (Brittany: Spearman's $r = 0.147$, $P = 0.346$, $n = 44$; Lozère, Spearman's $r = 0.294$, $P = 0.053$, $n = 44$).

We found no intrafamily selection to be acting on hatchling size and mass in Lozère (in 6 of 19 families, surviving hatchlings had a greater SVL than non-surviving sibs, binomial test $P > 0.1$; in 12 of 25 families, surviving hatchlings had a greater body mass than non-surviving sibs, $P > 0.1$; in 12 of 22 families, surviving hatchlings had longer tails than

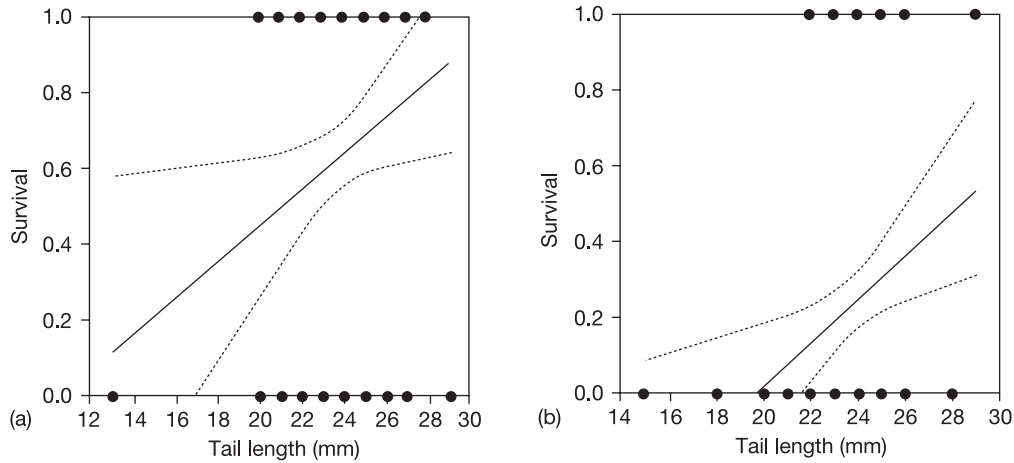


Fig. 2. Relationship between survival and tail length in Lozère (a) and Brittany (b). Symbols as in Fig. 1.

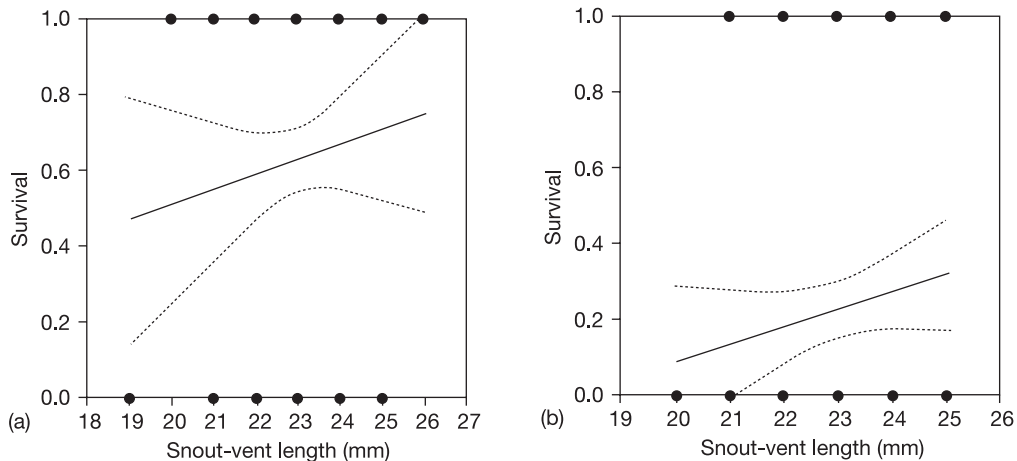


Fig. 3. Relationship between survival and snout-vent length in Lozère (a) and Brittany (b). Symbols as in Fig. 1.

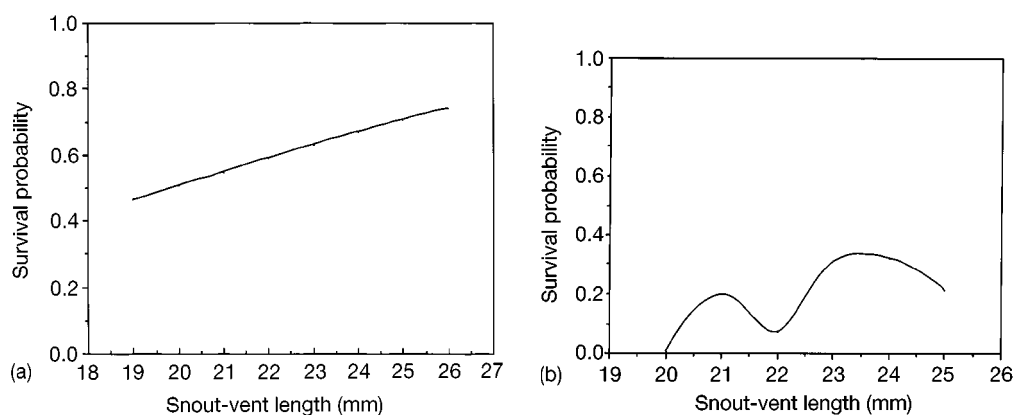
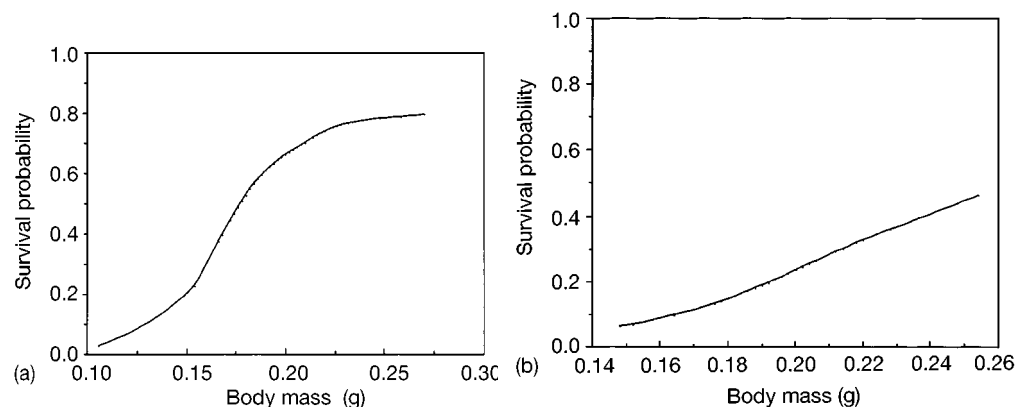
non-surviving sibs, $P > 0.1$). In Brittany, surviving hatchlings were heavier and had longer tails than their non-surviving sibs (in 8 of 12 families, surviving hatchlings had a greater SVL than non-surviving sibs, binomial test $P > 0.1$; in 11 of 15 families, surviving hatchlings had a greater body mass than non-surviving sibs, $P = 0.036$; in 10 of 13 families, surviving hatchlings had longer tails than non-surviving sibs, $P = 0.022$).

Patterns of selection on morphological traits did not differ between the two sites. We used a multivariate log-linear model to test the interaction between the selection environment and both a linear and z -transformed squared term of each morphological trait. We found no significant interactions between the selection environment and hatchling body mass, snout-vent and tail length (log-linear model: $SVL \times \text{site}$, $\chi^2_1 = 0.32$, $P = 0.571$; $\text{mass} \times \text{site}$,

Table 3. Standardized stabilizing differentials (c) and their significance (P) for body mass, snout-vent length and tail length at the two sites (Lozère and Brittany)

	Brittany			Lozère		
	c	P^a	P^b	c	P^a	P^b
Body mass	-0.046	0.074	0.080	-0.043	0.224	0.213
Snout-vent length	-0.042	0.226	0.394	0.006	0.400	0.664
Tail length	-0.006	0.341	0.602	-0.044	0.139	0.187

^a Significance by randomization tests (see Methods). ^b Significance by logistic regression.

**Fig. 4.** The cubic spline estimate of the fitness function (Schluter, 1988) for snout-vent length in Lozère (a) and Brittany (b).**Fig. 5.** The cubic spline estimate of the fitness function (Schluter, 1988) for body mass in Lozère (a) and Brittany (b).

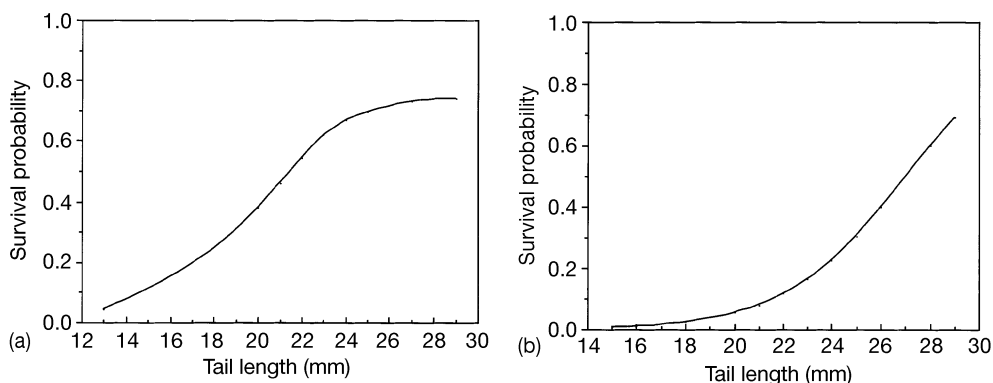


Fig. 6. The cubic spline estimate of the fitness function (Schluter, 1988) for tail length in Lozère (a) and Brittany (b).

$\chi^2_1 = 0.01$, $P = 0.912$; tail*site, $\chi^2_1 = 1.10$, $P = 0.294$; squared SVL*site, $\chi^2_1 = 1.53$, $P = 0.217$; squared mass*site, $\chi^2_1 = 0.30$, $P = 0.584$; squared tail*site, $\chi^2_1 = 0.21$, $P = 0.649$), suggesting that, overall, patterns of selection on hatchling morphology were the same in the two environments.

Finally, we found no significant differences in hatchling snout-vent length, body mass and tail length of survivors at the two sites (t -test: snout-vent length, $t_{100} = 0.814$, $P = 0.417$; body mass, $t_{100} = 0.453$, $P = 0.652$; tail length, $t_{100} = 1.113$, $P = 0.268$), again suggesting similar patterns of selection between the two environments.

Selection on mothers

Differential mortalities of hatchlings may have a direct effect on the optimal maternal investment in reproduction (e.g. litter size). In this scenario, the target of selection may shift from hatchlings to mothers. We tested this by estimating (1) the trade-offs between litter size and hatchling body mass, size and tail length, and (2) the correlation between litter size and the proportion of surviving sibs per litter.

Litter size was significantly negatively correlated with hatchling body mass and body size, after partialling out mother's body size (body mass: Pearson's $r = -0.388$, $P = 0.010$, $n = 44$; body size: Pearson's $r = -0.382$, $P = 0.012$, $n = 44$), whereas it was not correlated with tail length (Pearson's $r = -0.095$, $P = 0.543$, $n = 44$). Litter size was not a good predictor of hatchling survival at either site (Brittany: Spearman's $r = -0.200$, $P = 0.197$, $n = 44$; Lozère: Spearman's $r = 0.005$, $P = 0.974$, $n = 44$). This result was confirmed by a stepwise logistic regression model in which the proportion of surviving hatchlings per litter was a function of litter size, z -transformed squared litter size, and mother's SVL. None of these variables was significantly correlated with survival at each site (all $P > 0.19$).

DISCUSSION

Both hatchling body mass and tail length were under directional selection at the two sites studied. Conversely, hatchling snout-vent length was not significantly correlated with survival. We did not find any evidence of stabilizing or disruptive selection acting on

hatchling morphology. There was no significant interaction between the sites and the morphological traits considered here, which suggests similar patterns of selection at the two sites. Finally, we did not find any correlation between litter size and hatchling survival.

In most reptile species, juveniles are completely independent of parents immediately after birth (de Fraipont *et al.*, 1996). This lack of parental care imposes strong selection pressures because hatchlings must, in a short space of time after hatching, adapt to a novel environment, catch prey, escape predators, and avoid competition with both conspecific and non-conspecific individuals. A large body mass at birth may result in a high probability of survival because fatter individuals are better prepared to face periods of starvation, to avoid predators, or invest in antiparasite immune responses. Alternatively, a large body mass may simply reflect a better general body condition and hence correlate positively with survival, although the direct target of selection is another trait. Tail length can also be considered a general index of body condition in lizards, since the tail is used to stock energy reserves (Bellairs and Bryant, 1985) that can be used when food becomes rare or competition increases. The importance of tail energy reserves and the cost of tail regeneration in the common lizard have recently been demonstrated. Lizards infected with blood parasites have lower tail regeneration than parasite-free individuals (Oppliger and Clobert, 1997).

We found no evidence of selection acting on snout-vent length. This is surprising given that most previous studies dealing with selection on body size in reptiles reported directional or stabilizing selection on this trait (Fox, 1975, 1978; Ferguson *et al.*, 1982; Ferguson and Fox, 1984; Jayne and Bennett, 1990; Sinervo *et al.*, 1992; Janzen, 1993; but see Forsman, 1993). One possible explanation for a lack of correlation between snout-vent length and survival in the common lizard could be that this character shows very low variability ($CV = 5.13$), and natural selection needs variability to act (Endler, 1986). This reduced phenotypic variance may be the result of strong selection pressures, which may have acted both on juvenile snout-vent length and maternal investment in offspring in the past. A series of experiments in which density and food availability were manipulated in this species failed to find any effect on hatchling SVL, whereas other morphological, behavioural and life-history traits were affected by the environmental manipulation (Clobert *et al.*, 1994; Sorci and Clobert, 1997; J. Clobert, M. Massot and G. Sorci, unpublished). These results support the hypothesis that hatchling SVL might be constrained by some internal factor, such as the available volume in the mother's abdomen. Alternatively, it could be that selection pressures acting on SVL are weaker than for the other traits, and thus much larger sample sizes would be needed to detect such a weak effect. In this respect, it is worth noting that, overall, the differences between survivors and non-survivors in traits showing significant selection were small, suggesting weak selection strength. As noted above, however, this may be the result of previous selection forces acting on these traits, which may have eroded their variability. New techniques have recently been used to overcome this problem by increasing phenotypic variation of selection targets (Sinervo *et al.*, 1992; Janzen, 1993).

Life-history theory assumes that organisms cannot increase the allocation of limited resources to reproduction without diverting energy from another competing function (Sibly and Calow, 1986; Roff, 1992; Stearns, 1992). This allocation principle leads to trade-offs between life-history traits. For instance, maternal investment on reproduction, measured as the number of propagules produced, is usually traded against propagule size (Stearns, 1992). Given that propagule size is likely to affect survival prospects, we could expect that parents adjust their reproductive investment to maximize propagule survival.

In this scenario, selection might act directly on parental investment. Our study provided evidence to support the view that litter size is traded against hatchling body size and mass. However, we did not find any correlation between litter size and hatchling survival, suggesting that there is no direct selection operating on litter size. However, we remind readers that litter size ranged from 4 to 8 in our sample and it is possible that counter-selection operates only at lower or higher fecundities.

The two environments considered here appear to impose the same selective regimes on hatchling morphology in the common lizard. This is surprising given the differences in both the physical characteristics of the two environments and the differences in the life histories of the individuals inhabiting them (Bauwens *et al.*, 1986; Sorci *et al.*, 1996a). In other reptile species, fluctuating patterns of selection have been reported both in time and space. Using an allometric engineering experiment, Sinervo *et al.* (1992) investigated the relationship between fecundity, egg mass and hatchling survival in the lizard *Uta stansburiana* in two localities over 2 years. They found different patterns of selection on egg mass between localities, years and even different clutches within a year. The shape of the relationship between hatchling survival and egg mass varied from linear positive to linear positive and squared negative (Sinervo *et al.*, 1992). Fluctuating selection in time has also been reported for the adder (*Vipera berus*) in Sweden, where body size is positively correlated with survival in some years and negatively correlated with it in other years (Forsman, 1993).

The present study was conducted over a much shorter period of time and therefore it is possible that, over longer periods, selection may differ between the two environments. However, we considered one of the most critical periods for juvenile survival, the time between birth and first hibernation – the average mortality during the first month of life is 40% (J. Clobert, M. Massot and G. Sorci, unpublished). Moreover, the finding of similar selection regimes at the two sites is in line with the results of similar experiments, which showed that individuals transplanted to Brittany differed in both life history and morphology from individuals that remained at the Lozère site (Sorci *et al.*, 1996a). Moreover, these results also show that the transplanted hatchlings acquired the same phenotypic characteristics of the lizards naturally occurring in Brittany – that is, a low survival rate and a high growth rate. This suggests that the observed phenotypic plasticity was induced by some predictable environmental cues (e.g. temperature). A companion experiment in which hatchlings from both the Lozère and Brittany populations were raised in a common laboratory environment has, furthermore, shown that the observed differences in growth rate for the natural populations disappear when the environmental conditions faced by the hatchlings are the same (Sorci *et al.*, 1996a). These results, together with the finding of similar patterns of selection, support the view that the geographic variation in life-history traits in these two populations of the common lizard may be the result of phenotypic plasticity.

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