Oecologia (1999) 118:423–430

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Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*)

Received: 8 June 1998 / Accepted: 16 November 1998

Abstract We investigated the effect of water constraints on yearling *Lacerta vivipara*, a widespread species of lizard inhabiting European peat bogs and heath land. We conducted a laboratory experiment to investigate plasticity of growth rate, activity level and preferred body temperature. We subjected individuals of two source habitats (dry vs humid) to two laboratory conditions of water supply resulting in different air relative humidity and water availability (high vs low). We observed that a low water supply induced a lower growth rate and lower activity level, suggesting that growth limitation is correlated with adaptive responses to avoid dehydration. However, individuals from the two habitats selected different body temperatures when restricted in water and showed different ratios between growth and activity. This suggests that there is population variability in phenotypic plasticity with respect to water availability in the habitat. Field observations conducted in six natural populations, classified into two groups (dry vs humid habitat) also suggest that growth rate in nature is constrained by water availability.

Key words Adaptation · Behavioural response · Environmental constraints · Phenotypic plasticity

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Introduction

The environment is an important cause of variation in morphological and life history traits of organisms (Via and Lande 1985; Sultan 1987; Gebhardt and Stearns 1993). Interactions between an organism and its environment can lead to phenotypic plasticity which includes both adaptive and non-adaptive responses (Gotthard and Nylin 1995; see also Smith-Gill 1983). In addition, the shape of the reaction norm under a set of environmental conditions may reflect genetic variability among individuals, and may be subject to selection (Stearns 1989). Thus the reaction norm may itself be an adaptation. These issues have been addressed in various biological systems. For example, many studies have investigated the effects of food availability, thermal conditions or photoperiod on development, growth and reproduction (e.g., insects: Leimar 1996; fishes: Jonsson et al. 1996; amphibians: Claussen et al. 1983; reptiles: Sinervo and Adolph 1989; birds: Konarzewski et al. 1996).

Phenotypic plasticity of growth rate has been the focus of a large number of studies because this trait is a key determinant of age at maturity, fecundity and survival (Bauwens and Verheyen 1985; Ferguson and Talent 1993; Clobert et al., 1998). Growth rate has been found to respond to food availability and thermal conditions in ectotherms (Dunham 1978; Jones et al. 1987; Sinervo and Adolph 1994), and these responses may explain part of the geographical variability observed for this trait in many species (Sinervo and Adolph 1994; Sorci et al. 1996). Indeed the thermal environment defines the range of temperatures achievable by an individual and therefore the activity level and the rate of many physiological processes, such as food acquisition and conversion (Van Damme et al. 1991). The joint responses of these traits to temperature were investigated and modelled by Adolph and Porter (1993).

Water is also an important resource because it is involved in many physiological processes. Physiological studies have provided abundant information on osmoregulation and on mechanisms of water conservation (review: Minnich 1982; Nagy 1982), but these studies mainly involved species living in extreme conditions such as deserts or aquatic environments. According to physical laws, evaporation increases when temperature increases, suggesting a strong interaction between thermoregulation and water balance in ectotherms (Mautz 1982). However, little is known about phenotypic variability of life history traits induced by water availability. Are there adaptive responses to constraints in the hydric environment? Could water be a limiting factor for growth rate? The influence of water availability has generally been considered to be indirect because food abundance is often correlated with precipitation level so that the effect of water availability is confounded with the effect of food availability (Dunham 1978). However, Stamps and Tanaka (1981) showed that juvenile growth rates of the tropical lizard *Anolis aenus* were directly affected by water availability and that water scarcity explained most of the growth rate limitation during the dry season. In the event of a water shortage, some lizards exhibit lower body temperatures and may modify their activity patterns (Huey and Webster 1976; Crowley 1987; Jones et al. 1987).

We postulated a link between growth limitation and change of activity pattern that would be apparent on two different time scales (activity pattern: minutes to hours; growth rate: weeks to months). We predicted that individuals would respond to water shortage by changing their activity pattern. This change could affect body temperature and thus growth as already observed when individuals are under a thermal constraint (Andrew 1982; Grant and Dunham 1988; Avery and Mynott 1990; Adolph and Porter 1993).

We tested these predictions in the common lizard (*Lacerta vivipara* Jacquin), a species spread widely from northern Spain to the Pacific coast of Russia, and from Scandinavia to southern Romania. Its habitat varies from quite dry heath land to humid peatbog, suggesting the potential adaptation to water availability. We conducted a laboratory experiment to investigate the effects of water availability on growth rate independently from food and heat availability. Sampling individuals in two contrasted habitats (dry vs humid), we tested for variability of the phenotypic plasticity (measured on growth rate and thermoregulation pattern) expressed under hydric constraint. Finally, we tested whether water availability was a limiting factor in natural conditions by comparing the growth rate of yearlings in six populations living in two different natural humidity levels.

Materials and methods

The species

L. vivipara is a live-bearing lacertid widespread in Europe and Asia. Life history traits vary within this large area according to climatic conditions (Bauwens et al. 1986; Pilorge et al. 1987). In the Massif Central (France), where our study took place, individuals are active between April and October and hibernation occurs between October and April. At birth, between July and August, individual snout-vent length (SVL) ranges from 20 to 25 mm. Reproductive maturity is attained after 2 years. Adult SVL ranges from 50 to 70 mm. Thus, compared to other age classes, growth rate is high for juveniles (born in the current season) and after the first hibernation for the yearlings (born the previous year). All of the lizards used in this study were yearlings.

Laboratory experiment

Yearlings were sampled between 12 and 15 June 1996 from Mont Lozère, (France, 44°30′N, 3°45′E): 39 individuals from a dry site (heath land, D1) and 37 individuals from a humid site (peatbog, H1). The two populations were separated by about 10 km. Each lizard was housed in an individual plastic terrarium (25 × 15 × 17 cm high) with about 1 cm of soil. A basking site and a shelter permitted daily thermoregulation. Heat was provided 6 h per day by an incandescent electric light bulb hanging at one end of the terrarium. Lizards were held on a natural photoperiod and were fed ad libitum with small crickets. The presence of crickets was checked every day and we topped up their supply as their numbers declined. All yearlings were individually marked by toe-clipping and then randomly assigned to two experimental treatments: hydrated and desiccated. To avoid block effects, we systematically alternated the terraria of the two treatments on each shelf of the racks so that there was no correlation between treatment group and potential thermal gradient in the room or within a rack. In the hydrated group, each terrarium was wetted at its cool side (away from the light bulb, designated the wet side) three times per day. In the desiccated group each terrarium was wetted only once, in the morning. Water was sprayed on the plastic wall of the terrarium so that drops could be used for drinking for about 1 h after spraying and soil and cardboard shelter were wetted for some hours. Thus both the air humidity and the available water were contrasted between treatments. In the hydrated condition, lizards had available water to drink three times in the day whereas in the desiccated condition, lizards could only drink in the morning. In the hydrated condition, the soil stayed wet all day long whereas in the desiccated condition, it dried in the afternoon. Resulting air relative humidity in the terrarium was quite similar in the morning (up to about 80%) but 75% for the hydrated group and 40% for the desiccated group in the afternoon (measured at the wet side). This range of humidity reflected natural conditions. We measured in the field the air relative humidity in different microhabitats with an electric probe (thermohygrometer, pen-type) located under the vegetation. The lowest values were found in heath land under *Calluna vulgaris* (35–50%) and the highest in humid meadows under herbaceous ground cover (60–70%). These microhabitats were actually used by free-ranging animals: in dry habitats, 74% of subadult captures occurred in *C. vulgaris* ($n = 93$), whereas in humid habitats, 92% of subadult captures occurred in herbaceous ground cover ($n = 259$). To ensure that the thermal gradient in the terraria was large enough to allow thermoregulation and that it did not strongly differ between the two treatments, we estimated the thermal range in the two treatments using copper models (Grant and Dunham 1988; Bakken 1992). We adjusted the size and colour of the model to those of *L. vivipara*. For the two groups, the operative temperature was maximal just under the lamp (about 35°C) and minimal under the shelter (15–20°C, equal to room temperature, because in the shadow there is no radiative source of heat, only conduction), without differences in the thermal range for the two treatments. This range of temperature includes the known preferred temperature for this species (28–33°C; Heulin 1987). Thus, differences in body temperatures would not result from different thermal constraints, but from the use of thermic resource.

SVL and body mass (W) were recorded at the beginning (SVL0, W0) and at the end of the experiment (1 month later) (SVL1, W1). All measurements were made by the same person. Individual behaviours were described according to the ethogram of Lecomte (Lecomte et al. 1993), at different days and times during the experiment (with a mean of 20 records per individual). We recorded the location of the yearling in the terrarium (with respect to the heat source), its posture (basking, resting, hiding) or activity (walking, eating, foraging). We defined two activity states according to the following rule: active lizards were lizards basking and moving (walking, eating, foraging); and inactive ones were lizards resting under the shelter or in shady place or hidden in the soil. Feeding, spraying or measuring body temperature could affect activity. Thus, activity records were made at least 1 h after any of these perturbations. Records were spread out during the time heat was provided. The order of record-taking was random so that each individual was observed at different times. Lizards of the two treatments were alternated so that there was no correlation between time of recording and treatment. We defined two types of microhabitat in each terrarium: cool and wet side (where the shelter was located) and hot and dry side (with the basking site). Therefore we used the location of the lizard to determine which microhabitat was used.

We also measured lizard body temperature with a cloacal probe (thermocouple T). All measurements of body temperature occurred within 20 s of capture. Activity status was also recorded just before a lizard was captured for body temperature measurement. Order of sampling was random and we also varied each day the time at which temperature was recorded.

Field observations

We distinguished two habitat types according to their humidity level. Then we selected three populations (replicates) for each habitat type, including D1 and H1, the two source populations for individuals used in the laboratory experiment. On 15 July, we captured 14 individuals in heath land (D1) and 23 in the peatbog (H1), and measured their body length. We could therefore compare the mean body length of yearlings between mid-June (when we captured lizards for the laboratory experiment) and mid-July. The two other study sites (H2, H3) of the humid habitat type were clearings crossed by small streams and were largely flooded in spring and late summer. The air relative humidity in the most frequented substrate ranged between 60% and 70% (in July). The two other study sites (D2, D3) of the dry habitat type were heath land which received only water from rain and dew. The air relative humidity in the main substrate ranged between 45% and 50% (in July). Between 15 June and 15 July 1996, we sampled 70, 49, 24 and 37 yearlings in H2, H3, D2 and D3 populations, respectively, and recorded their body length and mass. All these individuals were known to be different because the populations were followed by capture-mark-recapture for other purposes. For the few lizards recaptured more than once between 15 June and 15 July, we only retained the data of the last capture to ensure independence of data in the following analyses.

Statistical analysis

Laboratory experiment

Growth was expressed as the rate of length gain per day, (SVL1–SVL0)/30, (Andrew 1982). We excluded individuals regenerating their tail because energy allocation to tail regeneration may interact with SVL growth (Ballinger and Tinkle 1979). We also analysed mass gain, (W1–W0)/W0, and variation of corpulence (residual of the mass × length regression). We tested differences among treatment groups and populations using an analysis of covariance [general linear model procedure (Proc GLM); SAS 1992], with initial SVL as a covariate. We also included activity level (see below) as a factor to test its influence on growth rate.

We expressed individual activity level by the ratio of the number of records in which the lizard was 'active' (see above) to the total number of records concerning that lizard. The distribution of activity did not depart from normality (Shapiro-Wilk test, $P = 0.13$; Proc Univariate; SAS 1992). Differences between groups were tested with an ANOVA (Proc GLM; SAS 1992). To analyse the use of habitat, we compared the frequency of active and inactive lizards in each type of microhabitat (Proc Genmod, microhabitat and individual as factor).

For each lizard we calculated mean 'active' and 'inactive' body temperatures by averaging all temperatures recorded just after the corresponding behaviour. The mean body temperatures were compared with a *t*-test (paired comparison) and then separately analysed with an ANOVA (Proc GLM; SAS 1992) with treatment group (hydrated or desiccated) and population of origin as factors.

Field observations

Because too few individuals were captured more than once, we cannot estimate growth rate on individual basis. Thus, we estimated a mean daily growth rate (mm day^{-1}) in each population with a linear regression of SVL against time. We compared the slopes of these regressions (equal to growth rate, mm day^{-1}) using an ANCOVA of SVL (proc GLM; SAS 1992) with type of habitat and population (nested in habitat type) as factors and time as covariate. Significant time × habitat (or time × population nested in habitat type) revealed differences in growth rate between habitats (or populations). For each analysis of variance, homoscedasticity of residual values was tested with a Bartlett test. Normality of the residual distribution was tested with a Shapiro-Wilk test (Proc Univariate; SAS 1992).

Results

Laboratory experiment

Growth

Initially, lizards from the dry habitat (mean SVL = 33.4 mm) were larger than those of the humid habitat (mean SVL = 30.6 mm, *t*-test $P < 0.001$). Within each habitat type, the treatment groups did not differ for initial SVL (*t*-test, $P = 0.960$). The growth rate was slower for individuals with larger initial SVL (SVL0: $F_{1,55} = 14.6$, $P = 0.0003$). As predicted, the experimental lizards kept in a humid environment (hydrated group) grew faster (0.17 ± 0.07 mm day^{-1}) than those kept in a dry environment (desiccated group, 0.12 ± 0.05 mm day^{-1}), (treatment $F_{1,55} = 8.0$, $P = 0.0065$; Fig. 1). In spite of their larger initial SVL, lizards from dry habitats (heath land D1) grew more rapidly (0.16 ± 0.07 mm day^{-1}) than those from humid habitats (peat bog H1, 0.14 ± 0.07 mm day^{-1}), (population $F_{1,55} = 7.2$, $P = 0.0097$; Fig. 1). None of the interactions were significant. Corpulence did not vary significantly during the experiment (model with population and treatment effects $F_{3,54} = 0.4$, $P = 0.7$). This is consistent with the correlation between the increase in length and the increase in body mass ($F_{1,56} = 117$, $P < 0.001$, $r^2 = 0.68$).

Activity

The activity level depended on water availability (Fig. 1), with a significantly lower activity level in the desiccated treatment group ($F_{1,73} = 20.2$, $P < 0.001$). The activity level was higher for individuals from the peatbog than for those from the heath land ($F_{1,73} = 9.9$, $P = 0.002$). There was no significant interaction between treatment and population effects. The hot and dry microhabitat was more frequented when lizards were active (92% of observations, $n = 1084$) than when they were inactive (64% of observations, $n = 759$; $\chi^2_1 = 192$ $P < 0.0001$) with differences between individuals ($\chi^2_{75} = 242$, $P < 0.0001$).

To examine if differences in growth may be explained by the differences in activity level, we performed an ANCOVA with growth as the dependent variable and population, treatment, initial SVL and activity level as factors (population: $F_{1,54} = 12.5$, $P = 0.0009$; activity: $F_{1,54} = 9.6$, $P = 0.003$; initial SVL × activity: $F_{1,54} = 7.8$, $P = 0.007$; all other effects: $P > 0.05$). In particular, the treatment effect was not significant in the presence of activity level in the model. It follows that differences in growth may be explained by a direct effect of treatment as well as by an indirect effect of treatment though a modification of activity level. Finally, growth increased with activity level, but this effect varies with initial SVL, being stronger for smaller lizards (Fig. 2).

Body temperature

Body temperatures selected by active lizards ranged from 24.5°C to 31.3°C with a mean of 28.6°C (standard deviation 1.6°C), concordant with values found for this species in many studies on its thermoregulation. (Patterson and Davies 1978; Heulin 1987). Body temperature was significantly higher for active than for inactive lizards (mean difference ± SE = 1.9 ± 0.03°C; paired *t*-test: $t = 6.84$, $P < 0.001$, $n = 71$). For individuals from the heath land (D1), the body temperature achieved by active lizards was the same in the humid and desiccated treatment groups ($F_{1,36} = 0.06$, $P = 0.804$; mean ± SE = 28.9 ± 0.07°C). For individuals from the peatbog (H1), the body temperature achieved by active lizards was higher in the hydrated group compared to the desiccated group ($F_{1,35} = 4.6$, $P = 0.039$; mean ± SE: desiccated, 27.8 ± 0.07°C, hydrated, 28.9 ± 0.07°C).

Field growth rate

As expected, yearling SVL increased from mid-June to mid-July (time: $F_{1,285} = 580$, $P < 0.001$). Growth rate depended significantly on habitat type (interaction habitat type × time: $F_{1,285} = 5.2$, $P = 0.023$; Fig. 3). There was no significant difference in growth rate between populations (replicates) within each habitat type (interaction time $*$ population (habitat type) $F_{4,281} = 1.9$, $P = 0.103$; Table 1).

Body length showed high variability between populations in each habitat type [population(habitat type): $F_{4,104} = 8.43$, $P < 0.001$; Table 1] so that we cannot detect any differences between habitats (habitat type $F_{1,4} = 2.73$, $P = 0.9$). In particular, the two populations (D1 and H1) used for the laboratory experiment

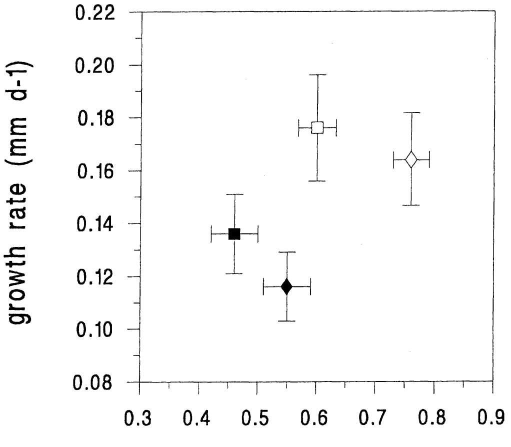

Fig. 1 Growth rate (mean ± SE) against activity level (mean ± SE) of yearling *Lacerta vivipara* of two populations (*diamonds* peat bog H1, *squares* heathland D1) under two conditions of water regime (*open symbols* hydrated group, *closed symbols* desiccated group). Each value represents between 13 and 20 individuals

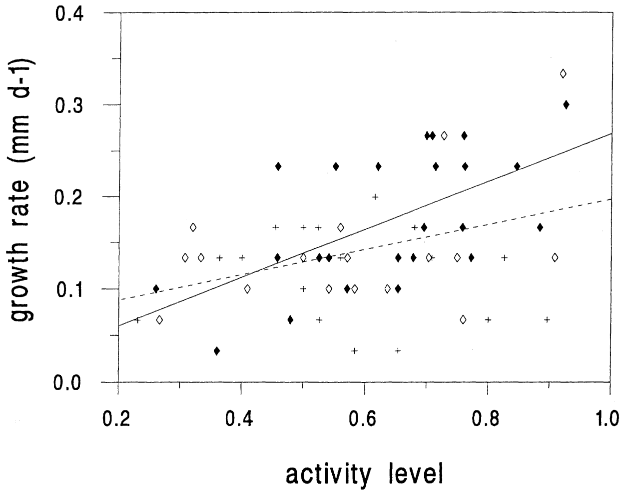

Fig. 2 Growth rate of *L. vivipara* yearlings as a function of their mean activity rate over the period of the experiment. The interaction between initial snout-vent length (SVL) and activity level is illustrated by dividing the lizards into three length classes: *closed diamonds*, *solid line*: small SVL0 class (SVL0 ≤ 31 mm), $F_{1,23} = 13.9$, $P = 0.0011$, $y = 0.01 + 0.26x$, $r^2 = 0.35$; *open diamonds*, *dashed line*: medium SVL0 class (31 mm < SVL0 ≤ 34 mm), $F_{1,14} = 6.1$, $P = 0.027$, $y = 0.06 + 0.14x$, $r^2 = 0.18$; *crosses*: large SVL0 class (SVL0 > 34), $F_{1,13} = 0.43$, $P = 0.5$

exhibited the largest sizes among populations of dry habitat type and the lowest sizes of humid habitat type, respectively. Therefore, the initial differences observed between the two populations might be largely explained by a sampling effect. This underlines the necessity of using replicates in each modality.

Discussion

We demonstrated that water scarcity can be a limiting factor for growth, even when lizards are well provided with food and access to heat. The experimental design actually altered hydric conditions (air humidity as well as water availability). Relative air humidity distinguished the two treatment groups and may have modified evaporative water loss. Indeed respiratory or skin water loss increases when water vapour density decreases in the environment (Mautz 1982), although we could not quantify this change in our experiment. Moreover, lizards in the hydrated group had more free-standing water to drink, and we saw them lapping droplets on the wall, demonstrating their need for it. It is unlikely that lizards of the desiccated group compensated the low water supply by water from their diet because they were less active and may have captured less prey. Metabolic water was also probably less abundant in the desiccated group because of an average slower metabolism due to a longer inactivity period. Thus, both water loss and water intake were affected by the treatment with reduced water availability for drinking in probably a major effect of the dessiccated treatment. Both physiological and behavioural mechanisms may help to mediate the growth limitation induced by water deprivation. Focusing our study on behavioural responses, we investigated selected body temperature and activity level as mediators of the changes in growth rate induced by water scarcity. First, we found that activity level varied with water availability (Fig. 1) and that the variation in activity level induced by the experimental conditions explained well the growth rate variability observed between the two treatments. Two questions must be discussed to interpret this result: (1) How is activity level related to hydric conditions (air relative humidity and water availability)? (2) Why does activity level affect growth rate? Second, we found that the activity level varied with source population and that peatbog individuals had a higher activity level but a lower growth rate. Thus, we will discuss the interpopulation variability of the response of growth rate to water scarcity and the relationship between constraints of local environment and natural variability of growth rate.

Table 1 Snout-vent length (SVL) and growth rate for the six populations of the field study. For H1 and D1, *n* includes the 37 and 39 lizards, respectively, used for the laboratory experiment. *Adjusted SVL* is the least-square mean deduced from the ANCOVA of SVL with time, population (nested in habitat type), habitat type and time × habitat type as effects. *Growth rate* is the slope of the regression of SVL against time calculated separately for each population

	n	Adjusted SVL (±SE) (mm)	Growth rate (±SE) (mm day^{-1})
Populations of humid habitat			
H1	60	35.6 (±0.3)	0.35 (±0.03)
H2	70	40.9 (±0.3)	0.42 (±0.04)
H3	49	37.8 (±0.4)	0.34 (±0.07)
Populations of dry habitat			
D1	53	37.8 (±0.4)	0.30 (±0.03)
D2	24	35.1 (±0.4)	0.34 (±0.03)
D3	37	34.9 (±0.5)	0.19 (±0.04)

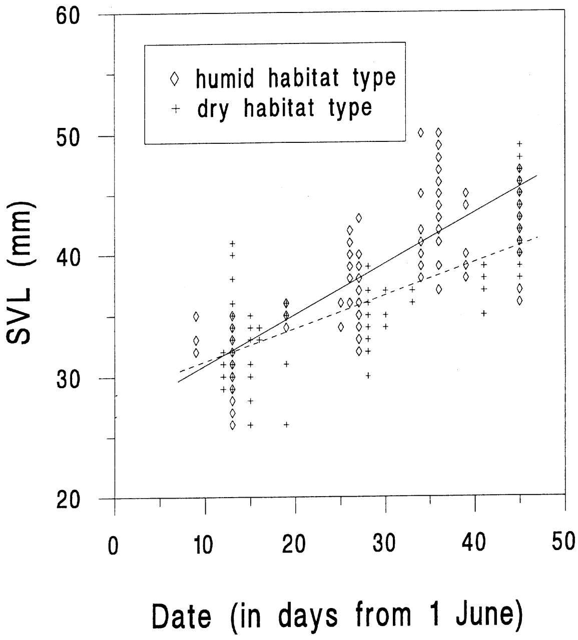

Fig. 3 Regression of body length (SVL) against time for *L. vivipara* yearlings sampled in natural populations. There were three populations for each habitat type. The slopes represent a mean daily growth rate (mm day^{-1}). The slopes are significantly different for the two habitat types ($F_{1,285}$ = 5.2, P = 0.023); humid habitats (*solid line* and *diamonds*): y = 26.7 + 0.42x, r^2 = 0.64; dry habitats: (*dashed line* and *crosses*): y = 28.7 + 0.27x, r^2 = 0.60)

Activity level and water availability

Experimental dry conditions reduced activity in lizards from both habitats. Such a result has already been found in two other lizard species (*Anolis aenus*; Stamps 1976) and *Sceloporus undulatus* (Crowley 1987; Jones et al. 1987). There are many reasons why this response may be adaptive. In a dry environment, lizards face a risk of dehydration. Our results suggested three ways in which lizards may avoid dehydration: (1) by decreasing their activity level, lizards of the desiccated group reduced their respiratory water loss, which is known to be substantial for many species of lizard (Mautz 1982); (2) lizards of the desiccated group spent less time at higher temperature (due to a longer inactivity period) thus reducing cutaneous water loss (Waldschmidt and Porter 1987); (3) the lizards selected non-desiccating conditions by using the high-humidity microenvironment when they became inactive. Such adaptive use of microhabitat in response to hydric constraint has been reported several times (reviewed in Mautz 1982). Individuals from the peatbog population also exhibit a lower preferred temperature when faced with dry than with humid conditions. In this case, water loss is a cost associated with thermoregulation that led lizards to achieve lower body temperature (Huey 1974). Crowley (1987) also demonstrated that water scarcity induces a lower preferred body temperature. Therefore, the hydration state of an individual should be considered as a constraint on the achievable body temperature, similar to the way in which solar radiation or wind speed are known to impose physical constraints on behavioural thermoregulation (Grant and Dunham 1988). However, there were no differences in body temperature between the two treatment groups for the heath land individuals. It is therefore not likely that the reduction in body temperature has a high contribution to the observed reduction in growth rate. Indeed, previous studies indicated a Q_{10} equal to 2.5 for the species *L. vivipara* between 25°C and 30°C (Al-sadoon and Spellerberg 1985), so that the observed difference of 1° Celsius between the preferred body temperature for peatbog individuals in the two treatments should result in a ratio between the metabolic rates of 1.1. The observed ratio between the growth rates measured in the hydrated and desiccated treatment for peatbog individuals (0.170 and 0.129) is equal to 1.3, higher than the 1.1 predicted by the simple effect of temperature on metabolic rate. Two interpretations are possible. Either allocation to growth is the same in the two treatments and the metabolic rate is directly reduced by water scarcity, or allocation to growth is reduced by water scarcity. However, in both cases, the treatment is found to have a distinct effect from temperature on growth.

Lowering activity level seems to be effective to face water scarcity and to avoid dehydration damage, but a likely cost of this behavioural shift would be a lowering of the growth rate.

Activity and growth

Seasonal and geographical variability of thermal conditions are known to affect the total time a lizard can be active at its preferred body temperature (Grant and Dunham 1988; Adolph and Porter 1993; Niewiarowski and Roosenburg 1993). In our experiment, activity was not directly affected by thermal conditions but mainly by water availability. Our results showed that a low activity level was associated with a low growth rate. Previous studies have suggested two mechanisms underlying the relationship between activity level and growth rate (Stamps and Tanaka 1981; Sinervo and Adolph 1994): (1) activity level is directly related to the time spent at a preferred temperature and therefore the time when physiological processes involved in growth (food digestion and assimilation, metabolism and conversion to somatic tissue) are most efficient (Huey 1982; Avery and Mynott 1990; Waldschmidt et al. 1986; Van Damme et al. 1991); (2) less active lizards may spend less time foraging so that the chance of encountering prey is decreased (Jones et al. 1987). This effect is probably stronger in field conditions than in the laboratory, especially when low water availability is associated with food shortage. By affecting both preferred body temperature and activity level, water limitation may indirectly affect growth rate.

Our findings suggest that the biological importance of avoiding dehydration is greater than the cost of lowering growth rate. Indeed, many physiological studies have underlined the severe consequences of dehydration (for instance, the serious cellular alteration due to hyperkalaemia; see Minnich 1982), whereas the actual cost of lowering growth rate is more difficult to establish. We know that individual body length influences fitness (survival and reproduction; Bauwens and Verheyen 1985; Ferguson and Talent 1993). However, in natural conditions, other factors may balance the decrease in growth rate such as the extension of seasonal activity period.

Interpopulation differences of response to water availability

Water shortage induced a lower activity level and a slower growth for individuals of the two populations (H1 and D1). Nevertheless, some differences were noted. First, as predicted, peatbog (H1) lizards had a higher activity level than heath land (D1) lizards, since their habitat of origin was characterised by a high level of humidity. But the ratio growth/activity was higher for D1 than H1 individuals even if the initial SVL of D1 lizards was greater, so that the growth rate differences between the two populations is reduced. This suggests that D1 individuals are more efficient during the activity period. This could be the sign of adaptation to water scarcity. Secondly, in the desiccated group, individuals from peatbog (H1) reduced their water loss by lowering their preferred body temperature by 1° Celsius. We did not find such a shift for individuals from D1, who responded to water scarcity only by lowering their activity level. In the investigated range of environmental conditions, D1 individuals did not show any plasticity for the preferred body temperature. This suggests that there may be some variability in phenotypic plasticity for activity level and preferred body temperature between populations. This variability in plasticity may just be due to a carry-over effect of a phenotype expressed earlier and itself under environmental control (Brown 1985; Fox and Savalli 1998), so that the individuals of the two habitats expressed different reaction norms. It can also be due to genetic differences between the two populations, which could have evolved under two different selective pressures with respect to local water availability.

Hormones are known to act on both growth and water balance (adrenal gland, Baverstock 1975; Firth and Turner 1982) or on both growth and activity level (thyroid gland, Gerwien and John-Alder 1992). Further investigations from the perspective of physiology may help us understand how adaptation to water scarcity evolves.

Field observations

From the results of the laboratory experiment, if water is actually a limiting factor in natural conditions, we predicted that individual growth rate should be lower in populations inhabiting dry compared to humid environments. In agreement with this prediction, we found that the mean SVL of individuals sampled in a dry habitat increased less rapidly than in those from a humid habitat. Field growth rates were also higher than growth rates in captivity but the results were consistent in the two approaches. Water constraint thus appeared to be effective in various environments and for different levels of growth rates, although its influence may vary quantitatively. Despite the different growth rates, the resulting body lengths in July did not differ between dry and humid habitats (habitat type: $F_{1,4} = 0.5$, $P > 0.5$; population (habitat type): $F_{4,104} = 8.43$ $P = 0.0001$, $n = 110$). This could be due to large SVL variability between populations of a given habitat type, suggesting that other factors affect body length, such as the length of the activity season. Yearling SVL depends not only on yearling growth rate but also on birth date, which determines the time a juvenile can be active before hibernation. It follows that the unexpected difference in initial SVL between individuals used in the laboratory experiment could be explained by particular conditions in the populations. Indeed, the peatbog population (H1) chosen for the experiment had the smallest individuals of all humid habitat populations and the dry population (D1) used for the laboratory experiment had the largest individuals among all dry habitats. Unfortunately, we have no information about the time of emergence from hibernation or on the food abundance for these populations sampled for the experiment. Nevertheless, we know that more snow accumulated in the peatbog than on heath land during March 1996. As a result, the melting took longer in peatbog than on the heath land. This suggests that activity may have begun later in the peat bog, thus explaining the observed differences in SVL. To disentangle the role of these different factors, we plan to manipulate the pre- and postnatal environment in order to identify the different ways in which water availability may affect individual characteristics and population demography.

Acknowledgements We thank E. Danchin, M. Massot and G. Sorci for helpful discussion and comments and P.H. Niewiarowski, R. Avery and an anonymous referee who critically revised a previous draft of the paper, and provided many constructive comments. We also thank the Parc National des Cévennes and the Office National des Forêts for providing facilities during our field work. This research has been supported by the Centre National de la Recherche Scientifique (CNRS).

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