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# A reciprocal transplant study of activity, body size, and winter survivorship in juvenile lizards from two sites at different altitude[1]

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*Abstract*: We examined activity rates prior to hibernation, age-adjusted body size, growth rates, and probability of recapture after spring emergence of juveniles from 2 populations of the lizard *Psammodromus algirus* separated by 600–700 m altitude. We captured gravid females, incubated the eggs, and released the juveniles into the wild. We used a reciprocal transplant design in a year of severe drought to distinguish between environmental and population-specific sources of variation. The levels of autumn activity differed between release sites (activity was higher at the more productive, high-elevation site) and between maternal sites of origin (at the low-elevation site, juveniles of low-elevation origin were less active than those of high-elevation origin). Although clutch mass was similar at both sites, eggs from low-elevation females were larger but fewer than those from high-elevation ones. Larger juveniles and those from high-elevation clutches had higher survival rates. The juveniles recaptured in autumn at the low-elevation site were smaller as neonates than those that were not recaptured until next spring. Our results suggest that the scarcity of prey at the low-elevation site is a selective pressure resulting in limitation of activity, given the increased energy expenditure and risk of predation incurred by active lizards. Thus, at the low-elevation site inactivity would be advantageous for most juveniles, and only the smaller ones would have to remain active frequently enough to accumulate sufficient reserves prior to hibernation. This is consistent with the selective advantage of large eggs (and small clutches) at the low-elevation site.

*Keywords*: drought, food scarcity, geographic variation, maternal trade-offs, *Psammodromus*, reproductive strategies.

*Résumé* : Nous avons examiné les taux d'activité avant l'hibernation, la taille corporelle ajustée selon l'âge, les taux de croissance et la probabilité de recapture après l'émergence au printemps des juvéniles de 2 populations du lézard *Psammodromus algirus* séparées par 600–700 m d'altitude. Nous avons capturé des femelles gravides, incubé les œufs et libéré les juvéniles dans la nature. Nous avons utilisé une expérience de transplantation réciproque lors d'une année de sécheresse sévère pour discriminer entre les sources de variation environnementale et spécifique de la population. Les niveaux d'activités automnaux différaient entre les sites de lâcher (l'activité était plus élevée au site le plus productif en haute altitude) et entre les sites d'origine maternelle (au site en basse altitude, les juvéniles originaires de ce site étaient moins actifs que ceux originaires du site plus élevé). Bien que la masse des couvées était semblable aux 2 sites, les œufs des femelles de basse altitude étaient plus gros mais moins nombreux que ceux des femelles d'altitude élevée. Les plus gros juvéniles et ceux des couvées de haute altitude avaient des taux de survie plus élevés. Les juvéniles recapturés à l'automne au site en basse altitude étaient plus petits à la naissance que ceux qui n'ont pas été recapturés jusqu'au printemps suivant. Nos résultats suggèrent que la pénurie de proies au site en basse altitude constitue une pression de sélection résultant en une limitation de l'activité, étant donné la dépense énergétique accrue et le risque de prédation encouru par les lézards actifs. Ainsi, au site en basse altitude, l'inactivité serait avantageuse pour la plupart des juvéniles et seulement les plus petits devraient rester actifs assez fréquemment pour accumuler des réserves suffisantes avant l'hibernation. Cette conclusion est compatible avec l'avantage sélectif des gros œufs (et des petites couvées) au site en basse altitude.

*Mots-clés* : compromis maternels, pénurie de nourriture, *Psammodromus*, sécheresse, stratégies reproductives, variation géographique.

*Nomenclature*: Linnaeus, 1758; Castroviejo *et al*., 1990, Montori & Llorente, 2005.

## Introduction

Natural populations of the same species living in different environments can differ in their life history traits as a response to variations in environmental conditions such as climate, food availability, or predator abundance (Martin, 1995; Shine, 2005; Brown & Shine, 2006). Among the characteristics that vary along environmental gradients (*e.g.*, latitudinal or altitudinal), clutch size, offspring size, growth rate, and size and age at maturity are crucial to understanding the ecology and distribution of animals. Reptiles provide excellent model systems for studying the evolution of these

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traits because the 2 main correlates of terrestrial ectothermy, low energy requirements and behavioural thermoregulation, have had major consequences for the evolution of reproductive strategies. For example, many of the life history features in which reptiles differ from birds and mammals, such as their smaller offspring sizes and larger litter sizes, reflect independence from heat-conserving constraints on body size and energy storage. This allows large flexibility in response to environmental conditions (Shine, 2005), so phenotypic plasticity is likely to be a more important component of life history variation in reptiles than in endothermic animals. In fact, lizards offer good opportunities to assess the relative contributions of phenotypic plasticity and genetic adaptation to among-population variation in life history characteristics. For example, differences in clutch size, egg size, growth rates, or adult body size may have resulted from the proximate effects of local conditions (*e.g.*, thermal opportunities or food availability) or from adaptive, genetically based responses to geographically variable selective regimes (Ballinger, 1979; Sinervo & Adolph, 1989; Adolph & Porter, 1993; Ferguson & Talent, 1993; Du, 2006).

Activity levels shape the relationship between environmental conditions and the life history phenotypes of ectotherms, acting as a filter that combines thermal opportunities with the amount of food available and the perceived levels of predation risk to yield the net amount of energy that is available for maintenance, growth, and reproduction (Rose, 1981; Adolph & Porter, 1993; Downes, 2001). Therefore, a lizard's activity is important for resource acquisition and growth. However, inactivity can also be adaptive because it usually decreases risk of predation and conserves energy (Adolph & Porter, 1993; Wilson, 1991; Sears, 2005). Thus, if predation risk is higher than feeding opportunities, one should expect low activity rates even when thermal conditions are suitable for activity (Rose, 1981), whereas the opposite should be true if food availability is high and predators are scarce.

For hatchlings from temperate climatic zones, activity prior to hibernation may be crucial. This is because their survival during the winter period depends on the resources allocated to them by their mothers during embryogenesis (*e.g.*, yolk quantity or quality) and on their capacity to grow prior to hibernation (Sorci & Clobert, 1999; Warner & Andrews, 2002). Energy reserves, activity, and growth opportunities for hatchlings may indeed modulate the maternal trade-off between clutch size and egg size (Niewiarowski & Dunham, 1994). When summer conditions predict a scarcity of food during the autumn, as is the case in xeric locations or in dry years, the optimum balance should be to produce fewer but larger offspring (Abell, 1999) that can remain inactive without severely compromising their winter survival. Alternatively, if there is abundant and/or high-quality food the production of larger clutches and smaller eggs might be favoured by fecundity selection (Ballinger, 1977; Warner, Lovern & Shine, 2007). It is therefore of interest to document the relationships between activity, growth rate, and survivorship in juvenile lizards of variable sizes that differ in the environmental conditions they experience early in life.

Within this context, reciprocal transplant experiments are useful to distinguish between the effects of the growing environment and the population of origin as sources of variation in the phenotypic traits examined (Niewiarowski & Roosenburg, 1993; Lorenzon, Clobert & Massot, 2001). We have previously reported the results of such an experiment (Iraeta *et al.*, 2006), in which we compared the growth rates of juvenile *Psammodromus algirus* lizards from 2 nearby populations separated by 600–700 m altitude in central Spain. We showed that although the growth rates of juveniles prior to hibernation were influenced by their mother's site of origin, the effect of the growing environment was clearly the most important one, overriding familial effects. Thus, juveniles grew faster at the more productive, high-elevation site (Iraeta *et al.,* 2006). In this study, we take advantage of the same reciprocal transplant experiment, combined with recapture data of the released cohort of juveniles the following spring, to accomplish the following goals: 1) to test whether the patterns described by Iraeta *et al.* (2006) are still valid after hibernation, *i.e.*, at 6–7 months of age; 2) to describe the allocation of the reproductive investment of females from both populations along the clutch size *versus* egg size trade-off; and 3) to discuss the effects of such allocation by disentangling the factors (*i.e.*, release site, site of origin, and size at hatching) that may affect autumn activity and/or winter survivorship of lab-born lizards released in the field immediately after hatching.

## Methods

### STUDY SPECIES

*Psammodromus algirus* is a medium-sized lacertid lizard (adult snout–vent length [SVL] 60–90 mm; mass 6–16 g) that inhabits shrub and woodland habitats of both margins of the Western Mediterranean basin (Arnold, 1987; Díaz & Carrascal, 1991). In central Spain, hibernation takes place from October through February, females lay eggs between April and June, and hatchlings are born in August–September (Veiga & Salvador, 2001). Clutch size and clutch frequency range between 3 and 12 eggs and between 1 and 2 clutches per year.

### STUDY AREAS

Our low-elevation study area was located at "El Pardo" (Madrid, central Spain: 40° 31' N, 03° 47' W; 650 m elevation; mean annual temperature = 12.5 °C), a holm oak (*Quercus ilex*) broad-leaved, evergreen forest. The high-elevation site was a deciduous Pyrenean oak (*Quercus pyrenaica*) forest located at Navacerrada (Cerro de la Golondrina, Sierra de Guadarrama, central Spain: 40° 44' N, 4° 00' W; 1300 m elevation; mean annual temperature = 6.2 °C), at a linear distance of 32 km from the lowland site. For a more detailed description of the study areas see Iraeta *et al*. (2006).

### HUSBANDRY OF ADULTS, EGGS, AND JUVENILES

Details of the husbandry of adult lizards, eggs, and juveniles can be found in Iraeta *et al.* (2006). In May 2005, 70 adult lizards (El Pardo: 22 gravid females and 11 males; Navacerrada: 26 gravid females and 11 males) were transported on the day of capture to the Department of Zoology (Universidad Complutense de Madrid), where they were housed in 60 × 40 × 30 cm terraria filled with moistened earth covered by leaf litter. A 60-W lamp suspended over one end of the cage created a ≈ 25–50 °C photothermal gradient allowing thermoregulation within the preferred temperature range (Díaz, Iraeta & Monasterio*,* 2006). Lizards were provided with food (crickets [*Acheta domesticus*] and mealworms [*Tenebrio mollitor*] dusted with a commercial vitamin and calcium supplement) and water *ad libitum*.

We monitored gravid females daily to detect egg-laying. Eggs were counted, weighed, and individually placed in 150-mL closed plastic cups filled with *ca* 35 g of moistened vermiculite (10 g vermiculite : 8 g water, equivalent to – 200 kPa). Eggs of the same clutch were distributed evenly over 2 incubators (Friocell, Königswinter, Germany) set at constant temperatures of 27 and 30 °C. This led to an experimental widening of the range of hatching dates (16 July – 18 August 2005). However, incubation temperature had no effect on growth rates of juveniles prior to hibernation (Iraeta *et al*., 2006), hatching success, or SVL at hatching (Iraeta, Díaz & Bauwens, 2007). Thus, we have ignored its effects in all remaining analyses. Newborns (sample size = 246 hatchlings: 117 from El Pardo [*n* = 19 clutches] and 129 from Navacerrada [*n* = 15 clutches]) were weighed, measured (SVL), and individually marked by toe-clipping before being released in the field the day after hatching. We used a split-clutch design both for incubation temperature and release site, releasing half of the hatchlings from a given clutch and incubator at the low-elevation site (*n* = 123) and the other half at the high-elevation site (*n* = 123).

### FIELD PROCEDURES

In September 2005 (5–29th) and between 28 February and 24 April 2006 both study sites were visited regularly, weather permitting, and all juveniles found while walking slowly across the study plots were captured. To control for hatchling dispersal, we expanded our search area to a 30-m-wide belt outside the plots (Civantos, Salvador & Veiga, 1999; Iraeta *et al.,* 2006). Recapture effort was 55.9 person-hours in 2005 and 36.0 person-hours in 2006 at the low-elevation site and 56.4 person-hours in 2005 and 42.0 person-hours in 2006 at the high-elevation site. Each captured lizard was examined to determine whether it was lab-reared or field-born. All lab-reared juveniles were measured (SVL) and weighed before being released once again at their site of capture. Growth rates were calculated as $\ln(SVL_2/SVL_1)/(\text{date } 2 - \text{date } 1)$ to reflect the proportionate increase in SVL from date 1 to date 2 on a per-day basis (Sinervo, 1990). A detailed account of sources of variation in growth rates between hatching and first recapture has been reported elsewhere (Iraeta *et al.,* 2006).

### ANALYSES

Because a relatively large fraction of the lizards captured in spring 2006 had not been detected in September 2005, we used the September recapture data as a proxy for hatchling activity prior to hibernation, and we classified lizards known to be alive (in the case of inactive ones, because they were recaptured the next spring) as active or inactive depending on whether they were or were not recaptured prior to hibernation. The reliability of this classification is supported by several lines of evidence. Although we did not tag recaptured lizards with unique paint marks, we marked them with a paint dot on the head to distinguish between lab-born individuals which had already been recaptured and those (either autochthonous or lab-born) that were seen for the first time. By the end of September, nearly all seen lizards at the low-elevation site had already been marked, and by mid-September, at least half of the marked individuals were repeatedly observed on different sampling days, as judged from the ratio between the number of different marked lizards seen on a given day and the number of lizards marked in previous dates. Thus, it seems that whereas some lizards were seen repeatedly, others were never observed, and it is reasonable to assume that those seen several times were active, whereas those not seen at all during the month of September but known to be alive could be classified as inactive.

In 2006, the sampling period was long enough to ensure that by its end all surviving juveniles should have emerged from hibernation. It should therefore be emphasized that whereas in September we used our recapture data of individuals as a surrogate for activity, in spring we used the recapture data as an indicator of survivorship, because after 2 months of regular visits at the beginning of the activity season most unobserved individuals must have emigrated or died. Although we cannot distinguish mortality from emigration out of our study area, the short distances moved by most marked individuals, and the low number of recaptures in the 30-m belts surrounding the study plots, suggest that emigration was unimportant. However, some individuals may have survived and remained in the study areas without being recaptured. This could confound our results only under the very unlikely assumption that recaptured and non-recaptured survivors had consistently different phenotypes. If non-recaptured survivors were similar to recaptured ones, in spite of which they were incorrectly classified as non-survivors, this would only decrease the power of our statistical tests, thus making our analyses conservative.

Unless otherwise stated, all statistical analyses were performed using general linear models after having checked the assumptions of normality and homogeneity of variances and, when necessary, log-transforming the corresponding variables. The effects of juvenile traits on winter survivorship were examined using logistic regressions with recapture data in spring 2006 as the dependent binomial variable. Data are given as mean ± 1 SE.

## Results

### BETWEEN-SITES VARIATION IN CLUTCH SIZE AND EGG SIZE

Low-elevation females laid smaller clutches than high-elevation ones (El Pardo: 5.8 ± 1.1 eggs, *n* = 19; Navacerrada: 6.9 ± 1.6 eggs, *n* = 15; $F_{1,\,32} = 5.0$, $P = 0.032$), but their mean egg mass was larger (El Pardo: 0.46 ± 0.06 g, *n* = 19; Navacerrada: 0.42 ± 0.05 g, *n* = 15; $F_{1,\,32} = 5.3$, $P = 0.029$). However, there were no differences in mean clutch mass (El Pardo: 2.69 ± 0.49 g, *n* = 19; Navacerrada: 2.85 ± 0.54 g, *n* = 15; $F_{1,\,32} = 0.8$, $P = 0.387$), which implies that the smaller size of the low-elevation clutches was compensated by the larger size of their eggs, and that the

2 populations made similar reproductive investments that they allocated differently along the clutch size *versus* egg size trade-off.

### RECAPTURE RATES BEFORE AND AFTER HIBERNATION

During the month of September more juveniles were recaptured at the high-elevation site (26 of 123) than at the low-elevation site (14 of 123; Iraeta *et al.,* 2006). However, these differences between release sites disappeared in spring, when we recaptured a similar proportion of lab-born juveniles at both sites (high-elevation: 27 of 123; low-elevation: 23 of 123; Fisher exact $P = 0.317$). Thus, the differences found prior to hibernation must be attributed to different activity rates rather than to differences in survivorship. In fact, 74% of the juveniles recaptured in spring at the low-elevation site had not been captured in September (17 of 23), whereas the same was true for only 33% of the juveniles (9 of 27) at the high-elevation site (Fisher exact $P = 0.0046$). This between-sites difference was mainly attributable to juveniles from low-elevation clutches (9 of 11 not captured in September at low-elevation *versus* 1 of 8 at high-elevation; Fisher exact $P = 0.0049$) rather than to juveniles from high-elevation clutches (8 of 12 not captured in September at low-elevation *versus* 8 of 19 at high-elevation; Fisher exact $P = 0.168$).

### SEASONAL AND BETWEEN-SITES VARIATION IN GROWTH RATES

We have previously shown that prior to hibernation, the high-elevation site provided more food and allowed hatchlings to grow faster and reach larger size, but also that juveniles from low-elevation clutches had larger growth rates and reached larger size when controlling for environmental effects (Iraeta *et al.*, 2006). However, these effects vanished during hibernation, because the growth rates between the September and spring recaptures did not differ significantly between sites of origin or release sites (site of origin: $F_{1, 20} = 0.28$, $P = 0.602$; release site: $F_{1, 20} = 0.21$, $P = 0.159$; origin × release site interaction: $F_{1, 20} < 0.001$, $P = 0.984$). As could be expected, growth rates between hatching and first recapture (Iraeta *et al.*, 2006) were higher than those registered between September 2005 and spring 2006 (Table I), especially at the high-elevation site, where growth rates decreased dramatically during hibernation (two-way ANOVA with period as a within-subjects effect and release site as a between-subjects effect; period: $F_{1, 22} = 24.81$, $P < 0.001$; release site: $F_{1, 22} = 16.24$, $P < 0.001$; interaction $F_{1, 22} = 8.20$, $P = 0.009$). Overall, the growth rate between hatching and next spring maintained the patterns reported for the pre-hibernation period (Iraeta *et al.,* 2006), being larger at the high-elevation release site and, to a lesser extent, also for juveniles from low-elevation clutches (release site: $F_{1, 45} = 40.72$, $P < 0.001$; site of origin: $F_{1, 45} = 3.72$, $P = 0.060$; interaction $F_{1, 45} = 0.92$, $P = 0.344$). Thus, the environmental difference between the 2 sites was still evident 6–7 months after hatching. As a consequence, at the beginning of their 2006 activity season there were significant differences in age-adjusted SVL both between release sites and between sites of origin (Figure 1), with larger differences in body size between juveniles of low- and high-elevation origin at the more productive, high-elevation site (two-way ANCOVA; effect of age: $F_{1, 44} = 39.33$, $P < 0.001$; release site: $F_{1, 44} = 37.12$, $P < 0.001$; site of origin: $F_{1, 44} = 32.89$, $P < 0.001$; interaction: $F_{1, 44} = 5.39$, $P = 0.025$).

However, we found no significant differences in age-adjusted SVL between juveniles from low- and high-elevation clutches released at their respective sites of origin (mean age-adjusted SVL in spring 2006 at high elevation: 35.0 ± 0.3 mm; low elevation: 34.6 ± 0.4 mm; effect of age: $F_{1, 27} = 49.03$, $P < 0.001$; site: $F_{1, 27} = 0.64$, $P = 0.431$). Thus, juveniles from high-elevation clutches released at their site of origin were able to compensate for their smaller size at hatching (mean SVL at hatching at high elevation: 27.7 ± 0.2 mm; low elevation: 28.2 ± 0.3 mm; $F_{1, 28} = 8.43$, $P = 0.007$).

### ENVIRONMENTAL AND POPULATION DIFFERENCES IN THE RELATIONSHIP BETWEEN SIZE AT HATCHING AND ACTIVITY PRIOR TO HIBERNATION

Since we assume that our September sampling effort was high enough to ensure that we managed to capture nearly all juveniles that displayed substantial levels of activity, we classified the juveniles recaptured in spring 2006 as active in September or not depending on whether they had already been recaptured prior to hibernation. A three-way ANOVA with size at hatching as the dependent variable and site of origin, release site, and activity prior to hibernation as classification factors (Table II) revealed a significant effect of site of origin (as expected, hatchlings from low-

TABLE I. Mean growth rate ($d^{-1}$) at high- and low-elevation release sites during the period until September 2005 and the period between September 2005 and spring 2006.

| Release site | Season | Growth rate ($d^{-1}$) | SE | *n* |
|---|---|---|---|---|
| High-elevation | Until September 2005 | 0.0030 | 0.00028 | 18 |
| | September 2005 – spring 2006 | 0.0006 | 0.00006 | |
| Low-elevation | Until September 2005 | 0.0011 | 0.00048 | 6 |
| | September 2005 – spring 2006 | 0.0004 | 0.00010 | |

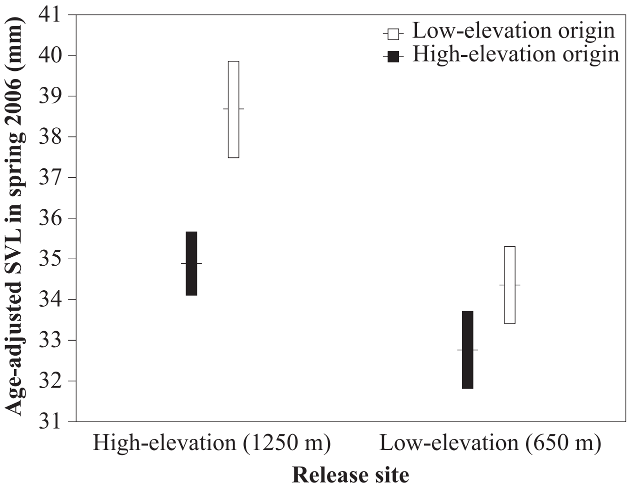

FIGURE 1. Age-adjusted body size after emergence from first hibernation (mean ± 95% confidence intervals) of laboratory-born juveniles from high- and low-elevation origin released at both study sites.

elevation clutches were larger) and a significant interaction between the effects of release site and activity in September: at the high-elevation site the juveniles that were recaptured in September were larger than the ones that were not recaptured, whereas the opposite was true at the low-elevation site (Table III). The three-way interaction was close to statistical significance (Table II), reflecting the fact that the two-way interaction was significant for juveniles from low-elevation clutches ($F_{1,\,15} = 5.78$, $P = 0.030$) but not for those from high-elevation clutches ($F_{1,\,27} = 0.18$, $P = 0.676$).

### Survivorship

A stepwise logistic regression with survivorship as the dependent variable and size at hatching, site of origin, release site, and all the interactions between these factors as independent variables generated a model that included only 2 predictors: size at hatching and site of origin (proportion of correct classifications = 0.79). According to this model, the probability of survivorship increased with SVL at hatching (Wald statistic = 10.53, df = 1, $P = 0.001$) and was higher for juveniles from high-elevation clutches (rate of survivorship = 0.24) than for those from low-elevation ones (rate of survivorship = 0.16; Wald statistic = 7.28, df = 1, $P = 0.007$), despite the larger size of the latter ones ($F_{1,\,244} = 42.4$, $P < 0.001$; Table IV). For the subsample of juveniles recaptured in September, growth rate prior to hibernation did not influence the probability of winter survivorship (Wald statistic = 0.67, df = 1, $P = 0.413$).

## Discussion

Our data showed that the juveniles differed in their activity levels prior to hibernation depending on 1) the site where they were released: overall, autumn activity was higher at the high-elevation site; and 2) their maternal site of origin: juveniles of lowland origin (with the exception of the smaller ones) were less active in autumn at the lowland site than juveniles of montane origin. In addition, larger juveniles and those from high-elevation clutches had higher survival rates. However, there were no differences in survivorship between release sites, despite higher productivity and higher growth rates at the high-elevation site.

When we analyzed the activity data separately for juveniles from different origins, activity levels prior to hibernation did not differ between release sites for lizards from high-elevation clutches. However, juveniles from low-elevation clutches showed different activity patterns at the 2 release sites, since they were active more frequently at the high-elevation than at the low-elevation site. Since activity is determined by environmental conditions (Adolph & Porter, 1993; Lorenzon *et al.,* 1999), perhaps juveniles from low-elevation origin responded more promptly to environmental conditions than juveniles from high-elevation origin, which maintained high activity levels at the low-elevation site despite its adverse conditions of severe drought and limited food availability (Iraeta *et al.,* 2006). An alternative explanation could be that most juveniles from low-elevation clutches were large enough to allow themselves to be inactive without lowering their energy reserves to the point of compromising their winter survival. In fact, at the low-elevation site the scarcity of prey may be a selective pressure resulting in limitation of activity, given the increased energy expenditure and risk of predation incurred by active lizards (Dunham, 1978; O'Connor, Sieg & Dunham, 2006). Consistent with that interpretation, the juveniles that were active prior to hibernation at the lowland site were smaller as neonates than those that were not recaptured before hibernation, and this difference was especially clear-cut for juveniles from low-elevation clutches. Thus, the smallest hatchlings might have been forced to be active to acquire enough resources prior to hibernation, whereas the benefits of inactivity might have prevailed for the majority of (larger sized) low-elevation juveniles. On the other hand, at the more productive high-elevation site (Iraeta *et al.,* 2006), size at hatching was similar for juveniles that were active and for those that were not recaptured prior to hibernation.

Between September 2005 and spring 2006, growth rates were almost negligible due to the winter diapause, and they did not differ between release sites or sites of origin. Thus, our data about growth rates between hatching and emergence from first hibernation confirm our previous finding (Iraeta *et al.,* 2006) that lizards grow faster at the high-elevation environment, because the difference in growth rates between release sites was still evident 6–7 months

Table II. Three-way ANOVA of SVL at hatching. SS = sum of squares; MS = mean square.

| Source of variation | SS | df | MS | *F* | *P* |
|---|---|---|---|---|---|
| Site of origin | 4.83 | 1 | 4.83 | 4.95 | 0.032 |
| Recaptured or not in 2005 | 0.03 | 1 | 0.03 | 0.03 | 0.855 |
| Release site | 0.26 | 1 | 0.26 | 0.26 | 0.610 |
| Origin × recapture in 2005 | 0.05 | 1 | 0.05 | 0.06 | 0.814 |
| Origin × release site | 0.56 | 1 | 0.56 | 0.57 | 0.454 |
| Release site × recapture in 2005 | 5.23 | 1 | 5.23 | 5.36 | 0.026 |
| Origin × recapture in 2005 × release site | 3.5 | 1 | 3.50 | 3.59 | 0.065 |
| Error | 40.99 | 42 | 0.98 | | |

Table III. Mean SVL at hatching (mm) of 2006 survivors as a function of site of origin, activity prior to hibernation (recaptured or not recaptured in 2005), and release site. Total numbers of spring recaptures: 19 juveniles from low-elevation origin and 31 from high-elevation origin; 23 recaptured at the low-elevation site and 27 at the high-elevation site.

| | | Low-elevation origin | | | High-elevation origin | | |
|---|---|---|---|---|---|---|---|
| Status in 2005 | Release site | Mean | SE | *n* | Mean | SE | *n* |
| Not recaptured | High-elevation | 28.0 | - | 1 | 27.5 | 0.27 | 8 |
| | Low-elevation | 29.1 | 0.26 | 9 | 27.8 | 0.31 | 8 |
| Recaptured | High-elevation | 29.6 | 0.48 | 7 | 27.8 | 0.38 | 11 |
| | Low-elevation | 27.5 | 0.50 | 2 | 27.8 | 0.25 | 4 |

Table IV. Mean SVL at hatching (mm) of survivors and non-survivors of high- and low-elevation origin.

| Site of origin | Survivorship | Mean | SE | *n* |
|---|---|---|---|---|
| High-elevation | Non-survivors | 27.2 | 0.13 | 98 |
| | Survivors | 27.7 | 0.17 | 31 |
| Low-elevation | Non-survivors | 28.2 | 0.13 | 98 |
| | Survivors | 29.1 | 0.26 | 19 |

after hatching. However, it is interesting to note that the size of the juveniles released at their corresponding site of origin did not differ between release sites, which is in contrast with the size difference found at hatching, when newborns from low-elevation origin were on average larger than those from high-elevation origin. Thus, although juveniles from high-elevation clutches grew at slower rates, the abundance of food at their site of origin allowed them to compensate for initial size differences in approximately 6–7 months. Remarkably, adults do not differ in size between the 2 populations (mean SVL data for the cohort of mothers and sires; El Pardo: 80.3 ± 0.6 mm, $n = 33$; Navacerrada: 80.7 ± 0.6 mm, $n = 37$; all $P > 0.65$ in the two-way ANOVA [not shown] with site and sex as factors).

Despite the harsh autumn conditions at the low-elevation site, no difference in survival between release sites was detected. This seems to indicate that the low activity levels shown by juveniles at low elevation was rather successful in promoting survivorship. Our data confirm previous reports that in *P. algirus* juvenile survivorship is positively influenced by body size (Civantos, Salvador & Veiga, 1999; Civantos & Forsman, 2000; Díaz *et al.*, 2005). However, and despite the larger size of hatchlings from low-elevation origin, the probability of being recaptured after hibernation was higher for juveniles from high-elevation clutches. Since activity time is correlated with resource acquisition (Adolph & Porter, 1993), a possible explanation for this unexpected pattern of winter survivorship could be that the juveniles from low-elevation clutches should be active more frequently to maintain their higher growth rates.

In turn, prolonged activity and rapid growth may have associated costs, which can be physiological (Metcalfe & Monaghan, 2001; Olsson & Shine, 2002) or ecological (*e.g.*, a higher probability of being predated; Rose, 1981; Adolph & Porter, 1993). However, our data on the animals recaptured prior to hibernation do not fully support this explanation, because the more active juveniles were from high-elevation origin (especially at the low-elevation site), and the growth rate during that period had no influence on winter survivorship. Therefore, there must be other reasons, not simply related to the costs of higher activity, for the lower survivorship of juveniles from low-elevation clutches. For example, early maternal effects during years of severe drought might compromise the winter survivorship of juveniles. It should be noted that although the females laid their eggs in the laboratory, early embryogenesis took place in the field, allowing the manifestation of environmental effects on the physiology of gravid females (Doughty & Shine, 1998; Warner, Lovern & Shine, 2007).

A last topic for discussion is that our findings are relevant to consideration of the egg size – clutch size trade-off within the ecological context of the costs and benefits of activity, which may be especially significant in Mediterranean climatic zones. Thus, in drought years juvenile lizards may face serious difficulties prior to hibernation, especially at xeric lowlands where food is scarce. In such scenarios, egg and hatchling size can modulate the chances of survival in different environments (Semlitsch & Gibbons, 1990; Sinervo *et al.,* 1992; Sinervo & DeNardo, 1996; Díaz *et al*., 2005; Díaz *et al*., 2007). Growing prior to hibernation at the low-elevation site may be extremely complicated in years of severe drought, due to food scarcity (and perhaps predation risk), and only large-sized juveniles would be able to remain inactive in order to survive the period prior to hibernation; this would select for smaller clutches of larger eggs. At the high-elevation site, however, fecundity selection would be free to favour larger clutches of smaller offspring (Díaz *et al*., 2007), because high food availability combined with thermal opportunities would allow hatchlings to remain active independent of their body size and to grow faster prior to hibernation. At the same time, habitats with high arthropod densities, as at our high-elevation site, would allow lizards to minimize the number of movements that might reveal their presence to potential predators (Díaz & Carrascal, 1993), and this would reduce the costs of activity while enhancing its benefits in terms of the energy accrued.

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