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Reproductive performance of a lacertid lizard at the core and the periphery of the species' range

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The range boundaries of organisms are frequently interpreted in terms of a decline in the extent to which the life histories of outer populations are able to adapt to local environmental conditions. To test this hypothesis, we compared the reproductive characteristics of two Iberian populations of the lizard *Psammodromus algirus* (Linnaeus, 1758). One of them (Lerma) is close to the northern edge of the species' range, whereas the other one (El Pardo) occupies a typical core habitat 200 km further south. Gravid females were captured in the field and transported to the lab for egg laying. Second clutches were less frequent at Lerma (where clutch size and clutch mass were larger for first than for second clutches) than at El Pardo. The total mass of both clutches combined was similar at both sites. Thus, the higher frequency of second clutches at El Pardo appeared to balance the between-sites difference in energy allocation to the first clutch. Females from Lerma laid more but smaller eggs than those from El Pardo. When incubated at the same temperature, eggs from Lerma hatched sooner even when controlling for between-sites differences in mean egg size. These differences are interpreted in the light of the advantages of early hatching and high fecundity in the northern population, as opposed to large offspring size in the core population. We conclude that the life-history traits studied show enough variation, presumably of an adaptive nature, to cope with environmental challenges at the edge of the species' range. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 87–96.

ADDITIONAL KEYWORDS: clutch size – egg size – life history – *Psammodromus* – range boundaries – reproductive investment.

INTRODUCTION

The size, shape, and boundaries of species' ranges reflect the interacting influences of limiting environmental conditions, dynamics of dispersal and extinction, and phylogenetic or palaeogeographical constraints (Brown, Stevens & Kaufman, 1996). In general, both the proportion of sites occupied and the average population density decrease from the centre to the edge of a species' range, which is usually interpreted as a consequence of the decline in habitat quality towards the edge of the range, or in the extent to which peripheral populations are able to adapt to local environmental conditions. A species will reach its range boundary wherever its dispersal is restricted by geographical barriers, such as at coastlines or near mountain ranges. However, when dispersal is apparently not limited, the emergence of range boundaries is more difficult to explain. In the absence of obvious barriers to dispersal, impaired environmental conditions at the periphery of the range, whether due

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to climate variation, the scarcity of important food resources, or the occurrence of predators, parasites or competitors (Hess & Losos, 1991; Downes & Bauwens, 2002), may end up reducing survivorship or breeding success, eventually making natality unable to balance mortality and giving rise to source-sink dynamics as the only way in which peripheral populations can persist (Pulliam, 1988; Blem & Blem, 1995). In turn, the ability of peripheral populations to cope with environmental challenges encountered across a geographical region where no obvious barriers to dispersal occur will determine the size, shape, and degree of fragmentation of the species' range within such region. If there is little life-history variation, dispersal from core areas will prevent the successful colonization of environments that would be more effectively exploited by acquiring other life-history strategy because all immigrants from core areas will be poorly adapted to local conditions. As a consequence, peripheral populations will remain maladapted and will only persist as a demographic sink. However, if the potential for life-history variation is large (due to genetic differences or to phenotypic plasticity), selection at the edge of the range may favour the local adaptation of peripheral populations (Pérez-Tris, Carbonell & Tellería, 2000; Carbonell, Pérez-Tris & Tellería, 2003). These two alternative scenarios have different consequences for the evolution of species' ranges, and local adaptation processes have been given a prominent role in the long-term persistence of species.

Nevertheless, and despite its important implications for management and conservation (Lawton, 1993), little attention has been paid to differences in life-history traits between peripheral and core populations. This is particularly noteworthy in the case of reptiles, whose low energy requirements and behavioural control of body temperatures not only determine their basic life-history traits (e.g. smaller offspring sizes and larger litter sizes than endothermic birds and mammals), but also allow huge variation in such traits via phenotypic plasticity or adaptation to local circumstances (Shine, 2005). Thus, it can be hypothesized that reptile populations living close to the latitudinal or altitudinal limits of their species' range should show different life-history strategies than those located closer to core areas. Life-history theory predicts that, once the allocation of resources to reproduction is fixed, natural selection can still shape the partitioning of that investment into a few large offspring versus many small ones (Smith & Fretwell, 1974; Sinervo & Licht, 1991; Stearns, 1992). As a consequence, peripheral populations could differ from central ones in: (1) overall reproductive investment; (2) partitioning of that investment; (3) reproductive phenology; and (4) degree of retention of eggs or embryos (viviparity has arisen at least 100 times within cold-climate populations of lizards and snakes; Shine, 2005).

Within this context, the present study aimed to compare some life-history characteristics (clutch frequency, clutch size, mean egg mass, clutch mass, and incubation time) of two populations of the lacertid lizard *Psammodromus algirus* (Linnaeus, 1758), which is probably the commonest reptile in the Iberian peninsula outside anthropic environments. It is only absent from the northern Cantabrian belt and from the highest Pyrenean altitudes, but apparently it is expanding its range along the Pyrenean valleys (Bauwens *et al.*, 1986). Thus, it appears to comprise a good model to explore the differentiation of reproductive characteristics in peripheral populations. For that purpose, and to reduce the inferential problems derived from the lack of replication, we carefully chose the populations to be compared. One population (Lerma) inhabits a mosaic landscape of forests and cereal fields close to the northern edge of the species' range. The other population (El Pardo) occupies a large Mediterranean forest situated near the centre of the species' Iberian range. The two study areas represent the typical conditions found by lizard populations at the northern boundary and the core area of the distribution range. After describing the differences between both populations in allocation of reproductive investment, we discuss the possible adaptive nature of such differences, and conclude that the life-history traits studied show enough apparent flexibility to cope with environmental challenges at the edge of the range.

MATERIAL AND METHODS

Study organism and study sites

Psammodromus algirus is a medium-sized (adult snout-vent length 65–90 mm; mass 6–15 g) lacertid lizard inhabiting shrub and woodland habitats of the Iberian Peninsula, south-eastern coastal region of France and north-west Africa (Díaz & Carrascal, 1991). It has a reproductive cycle typical of temperate species (Díaz, Alonso-Gómez & Delgado, 1994; Carretero & Llorente, 1997): females lay one or two clutches between April and July (spring–summer), and newborns appear between July and October (summer–autumn).

The northern study area (Lerma, approximately 70 km^2) was an agricultural landscape located in northern Spain (42°5′N, 3°45′W; 850 m a.s.l.), where environmental changes and historical agricultural practices have produced a mosaic of forest remnants interspersed among cereal fields. Forests form a mixed archipelago of deciduous (Pyrenean oaks *Quercus pyrenaica* Willd) and evergreen woods (holm oaks

Quercus ilex L.). We studied lizards from forests (unfragmented woodlots > 200 ha) and fragments (< 10 ha). A detailed report of the effects of fragmentation and forest type on lizard reproduction is provided elsewhere (Díaz *et al*., 2005); in the present study, the variance attributable to such effects is pooled within the error term, thus making our analyses conservative. Population densities of *P. algirus* are much smaller and more variable than at the southern area (J. A. Díaz, J. Pérez-Tris, T. Santos & J. L. Telleriá, unpubl. data). The site, close to the northern limit of the species' range in the Iberian Peninsula, has a mean temperature and a mean number of sunshine hours from March to October of 13.1 °C and 1798 h, respectively (average data for 1971–2000 at the nearby meteorological station of Burgos-Villafría).

The southern study site was located at El Pardo (Madrid, central Spain: 40°31′N, 03°47′W; 650–700 m a.s.l.), a holm oak (*Q. ilex*) broad-leaved, perennial forest of approximately 160 km^2. The shrub layer is dominated by offshoots of *Q. ilex* and by rockroses *Cistus ladanifer* L., alternating with open areas covered by annual herbs and/or bare ground. The site is located at the core of the species range in the Iberian Peninsula, and *P. algirus* reaches densities of approximately 30 adults/ha (Díaz, 1993). The mean temperature during the lizards' activity period (March–October) is 18.1 °C, and the mean number of sunshine hours is 2180 h (average data for 1971–2000 at the nearby meteorological station of Madrid-Retiro).

CAPTURE AND HUSBANDRY OF ADULTS

We captured lizards during the breeding seasons of 1995 (El Pardo, southern site), 2001 (Lerma, northern site), and 2002 (both El Pardo and Lerma), and brought them to the laboratory within 5 days of capture.

In 1995, animals (12 females and 12 males) captured at El Pardo were transported to Hasselt (Belgium) on 8 May. Upon arrival in the laboratory, each female was housed in a terrarium (100 × 40 × 40 cm), which it shared with a single male; copulations were observed frequently. The terraria, which were kept in a room which received natural daylight, had a substrate of moist sand, covered by a leaf litter layer that provided shelter together with several stones. A 120-W light bulb suspended above one end of the terrarium created a photothermal gradient allowing thermoregulation within the preferred thermal range. Food (crickets *Acheta domesticus*, and mealworms *Tenebrio mollitor*) and water were provided *ad libitum*, periodically supplemented with a vitamin mixture (A + D_3).

In 2001 and 2002, lizards [2001: 25 females and 24 males from Lerma; 2002: 29 females and 15 males from Lerma, and ten females and five males from El Pardo] were transported to the laboratory (Universidad Complutense, Madrid) between 21 May and 8 June We housed lizards in terraria (40 × 60 × 30 cm) with white opaque walls, covered by a green net (0.5-cm mesh) that prevented escape, let daylight enter the cages, and provided a shrubby-like shelter. Cages were filled with moistened earth covered by leaf litter. A 100-W lamp created a photothermal gradient allowing thermoregulation, and an earthenware tile and thin fallen wood provided shade and shelter. Lizards were fed crickets (*Acheta domesticus*), mealworms (*Tenebrio mollitor*) and wax-worms (*Galleria mellonella*) *ad libitum*, dusted with a commercial diet supplement. All cages were watered *ad libitum*. After all laboratory work had finished, lizards were released at their sites of capture.

HUSBANDRY OF EGGS AND JUVENILES

Our study species has the advantage that gravid females readily lay eggs in captivity, whereas their reproductive output reflects the environmental conditions experienced during the early stages of vitellogenesis (i.e. when the physiological coupling among clutch size, egg size and clutch mass occurs; Sinervo & Licht, 1991). We monitored the body mass and reproductive condition of gravid females daily. Immediately after laying, we removed the female, determined its post-laying body mass, and carefully searched for the eggs, which were counted, wiped clean of sand, and weighed to the nearest 0.01 g. We placed each egg in an individually labelled 150-mL plastic container filled with moistened vermiculite (8 g of water per 10 g of vermiculite, equivalent to –200 kPa). Eggs were completely surrounded by the vermiculite, and we closed the containers hermetically to minimize evaporation. We completed weekly inspections of all eggs to verify their gain of mass and their viability. Moisture was kept constant by adding water up to reach the initial mass of the moistened vermiculite. In 1995, eggs from El Pardo were distributed evenly over three incubators set at constant temperatures of 25.5, 27.0, and 30.5 °C (±0.5 °C), as part of a separate study of the phenotypic responses to egg incubation temperature (D. Bauwens & J. A. Díaz, unpubl. data), the results of which are not reported here. In 2001, incubation of eggs from Lerma took place at a more variable temperature of 29.5 ± 1.3 °C. In 2002, eggs from both localities were distributed evenly over two incubators set at a constant temperature of 30 ± 0.5 °C, thus providing data that allow to compare incubation times under identical thermal conditions.

At the end of incubation, we searched daily for newly-hatched lizards. Hatchlings were weighed and given unique toe-clip marks before being transported to nursery terraria where they were fed small crickets, dusted with commercial vitamins and a calcium supplement, for a variable period (2–6 weeks). Afterwards, they were released at the study areas (for a study of juvenile survival within the 2001 cohort, see Díaz *et al*., 2005).

DATA ANALYSES

We used analysis of variance (ANOVA) contrasts (planned comparisons) to compare the reproductive characteristics of females from El Pardo (1995 and 2002; contrast coefficient = –1) against those of females from Lerma (2001 and 2002; contrast coefficient = 1) while controlling for the effects of among-years variations. Thus, although no year–site interactions could be calculated due to missing cells, the between-sites effects were tested using the appropriate error terms.

First and second clutches were compared using two-way ANOVAs with population and clutch order as the main factors, and clutches (either first or second) as independent replicates. This allowed us to calculate the means ± SE using the whole data set, without excluding the females that laid only one viable clutch. However, we also performed repeated measures ANOVAs with population as the between factor, clutch as the within factor, and females as replicates (data not shown), and the results of both types of analyses produced exactly the same sets of significant effects.

When necessary, variables were log-transformed to meet the requirements of parametric tests. Data are reported as the mean ± SE.

RESULTS

SIZE AND CONDITION OF FEMALES

Females from Lerma were slightly larger than those from El Pardo (snout–vent length, SVL; Lerma: 74.9 ± 0.7 mm, $N = 54$; El Pardo: 72.0 ± 0.9 mm, $N = 22$; univariate test of significance for planned comparison: $F_{1,72} = 5.52$, $P = 0.022$), they were heavier at the moment of capture (field body mass, Lerma: 11.2 ± 0.3 g; El Pardo: 8.9 ± 0.4 g; $F_{1,72} = 19.1$, $P < 0.0001$), and they had a larger SVL-adjusted body mass [analysis of covariance (ANCOVA): $F_{1,71} = 17.6$, $P < 0.0001$]. This was probably due to a higher mass of the first clutch at Lerma, rather than to a better body condition, because neither postlaying body mass (Lerma: 8.5 ± 0.2 g; El Pardo: 8.0 ± 0.3 g; $F_{1,72} = 1.8$, $P = 0.182$), nor postlaying body condition (SVL-adjusted means; Lerma: 8.3 ± 0.1 g; El Pardo: 8.5 ± 0.2 g; $F_{1,71} = 1.1$, $P = 0.296$) differed significantly between both populations. Neither SVL, nor body mass at the moment of capture showed significant yearly variation in either population (all $P > 0.25$), but the postlaying body mass of females from El Pardo was slightly larger in 1995 than in 2002 (ANOVA: $F_{1,20} = 5.4$, $P = 0.031$).

FREQUENCY OF SECOND CLUTCHES

The frequency of second clutches was higher at El Pardo, where 64% of the females laid two clutches, than at Lerma, where only 22% of the females did so ($\chi^2 = 11.9$, d.f. = 1, $P = 0.0006$). Between-year differences were not significant in either case (χ^2, both $P > 0.1$). The frequency of inviable clutches (i.e. those in which no egg succeeded to hatch) was smaller for first (3%) than for second clutches (27%; $\chi^2 = 14.2$, d.f. = 1, $P = 0.0002$). However, hatching rates of clutches in which at least one egg succeeded to hatch were high and similar for first (hatching rate = 0.92 ± 0.02, $N = 74$) and second (0.87 ± 0.05, $N = 19$) clutches ($t_{91} = 1.04$, $P = 0.290$). In the remaining analyses, only viable clutches are considered. The egg mass data of two Lerma clutches that could not be weighed immediately after laying were not considered in the analyses.

MEAN EGG MASS, CLUTCH SIZE, AND CLUTCH MASS

Figure 1 shows the reproductive characteristics (mean egg mass, clutch size, and clutch mass) of first and second clutches from both populations. Mean egg mass did not differ between first and second clutches (two-way ANOVA; clutch: $F_{1,87} = 0.0002$, $P = 0.988$; population–clutch interaction: $F_{1,87} = 0.2$, $P = 0.663$). Females from Lerma laid more eggs in their first than in their second clutches ($F_{1,61} = 8.4$, $P = 0.005$), whereas females from El Pardo laid first and second clutches of a similar size ($F_{1,28} = 1.6$, $P = 0.218$; population–clutch interaction in the two-way ANOVA: $F_{1,89} = 8.3$, $P = 0.005$). As a consequence, clutch mass was larger for first than for second clutches in females from Lerma ($F_{1,59} = 4.8$, $P = 0.033$) but not in those from El Pardo ($F_{1,28} = 1.2$, $P = 0.274$; population–clutch interaction: $F_{1,87} = 5.5$, $P = 0.021$). This between-populations difference in energy allocation to the first clutch was not attributable to differences in body size. Instead, it was reinforced when controlling for the effects of female SVL (ANCOVAs with log-SVL as the covariate; Lerma, clutch effect: $F_{1,58} = 12.1$, $P = 0.001$; El Pardo, clutch effect: $F_{1,27} = 0.4$, $P = 0.553$; population–clutch interaction in the two-way ANCOVA: $F_{1,86} = 6.9$, $P = 0.01$). Thus, gravid females from Lerma had a larger prelaying body mass than those from El Pardo due to their higher investment in first clutches. Overall reproductive investment per female (total mass of both clutches) was similar at

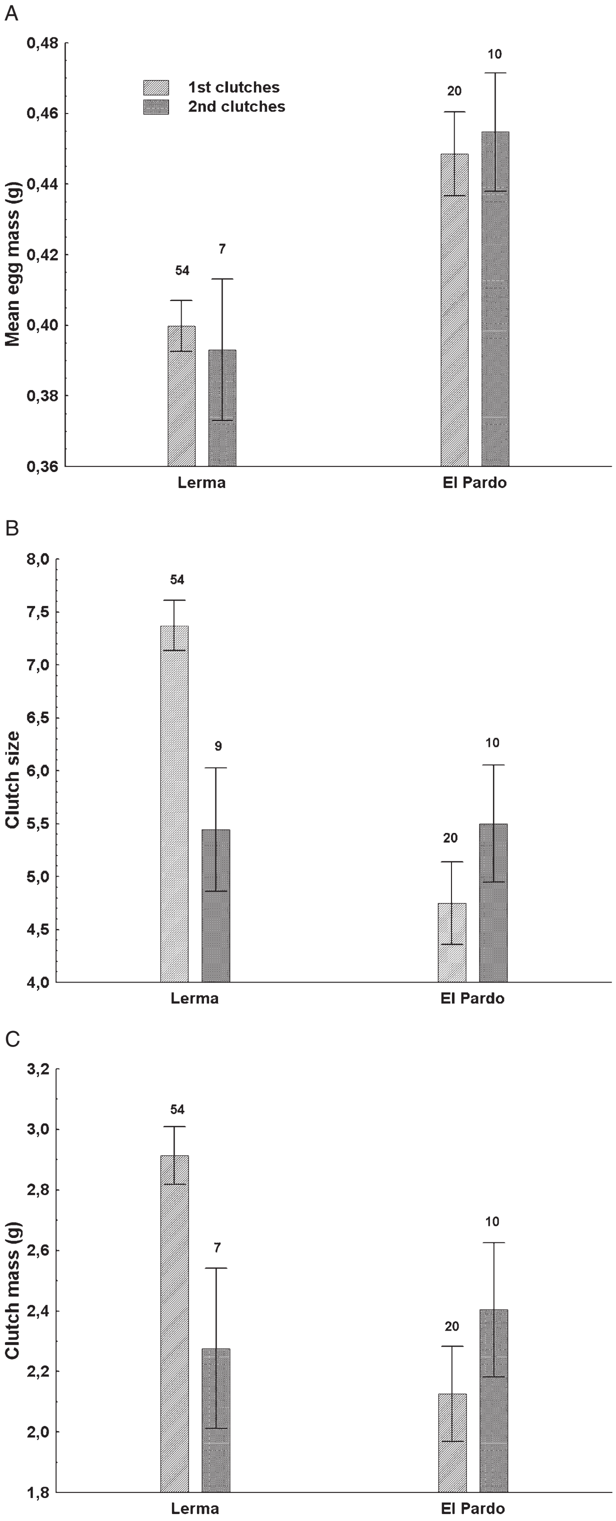

Figure 1. Mean ± standard error of first and second clutches laid by northern (Lerma) and southern (El Pardo) females for mean egg mass (A), clutch size (B), and clutch mass (C). Sample sizes are shown above the whiskers.

both sites (Lerma: 3.2 ± 0.2 g; El Pardo: 3.0 ± 0.3 g; $F_{1,70} = 1.4$, $P = 0.236$), also when controlling for the effects of female SVL (SVL-adjusted means; Lerma: 3.1 ± 0.16 g; El Pardo: 3.3 ± 0.25 g; $F_{1,69} = 0.02$, $P = 0.887$). Thus, the higher frequency of second clutches at El Pardo balanced the between-sites difference in energy allocation to the first clutch.

CLUTCH SIZE VERSUS MEAN EGG SIZE

Females from Lerma laid more eggs than those from El Pardo (mean clutch sizes; Lerma: 7.1 ± 0.24 eggs, $N = 63$; El Pardo: 5.0 ± 0.28 eggs, $N = 30$; $F_{1,89} = 24.8$, $P < 0.0001$; this is a conservative analysis because first and second clutches from Lerma are pooled together despite the smaller clutch sizes of the latter ones), but their mean egg mass was smaller (Lerma: 0.40 ± 0.01 g, $N = 61$; El Pardo: 0.45 ± 0.01 g, $N = 30$; $F_{1,87} = 16.3$, $P = 0.0001$). The mean body mass of juveniles at hatching was also smaller at the northern population (Lerma: 0.54 ± 0.01 g, $N = 63$; El Pardo: 0.58 ± 0.01 g, $N = 30$; $F_{1,89} = 6.3$, $P = 0.014$), as a consequence of the between-sites difference in mean egg size (ANCOVA with mean egg mass as the covariate; population effect: $F_{1,86} = 1.5$, $P = 0.229$; egg mass effect: $\beta = 0.864$, $F_{1,86} = 173.4$, $P < 0.0001$). These contrasting patterns of energy allocation along the clutch size versus egg size trade-off can not be attributed to differences in body size because they are still significant when controlling for the effects of female SVL (ANCOVAs; clutch size: $F_{1,88} = 18.7$, $P < 0.0001$; mean egg mass: $F_{1,86} = 14.6$, $P = 0.0002$). Neither clutch size, nor SVL-adjusted clutch size showed significant yearly variation at Lerma or El Pardo (all $P > 0.450$). Mean egg mass and SVL-adjusted mean egg mass did not differ significantly between years at Lerma (both $P > 0.440$), whereas at EL Pardo they were slightly smaller in 2002 than in 1995 (mean egg mass: $F_{1,28} = 4.4$, $P = 0.046$; SVL-adjusted mean egg mass: $F_{1,27} = 5.2$, $P = 0.031$).

Multiple regressions showed that in both populations clutch size increased with maternal SVL (Lerma: $\beta = 0.624$, $N = 61$, $P < 0.0001$; El Pardo: $\beta = 0.411$, $N = 30$, $P = 0.014$) and decreased with mean egg mass (Lerma: $\beta = -0.352$, $P = 0.0004$; El Pardo: $\beta = -0.375$, $P = 0.024$). To control for variation in maternal body size, we calculated the residuals from the regression of clutch size on female SVL. This index of size-adjusted fecundity was negatively correlated with mean egg mass at both Lerma ($r = -0.442$, $P = 0.0004$) and El Pardo ($r = -0.416$, $P = 0.022$), reflecting the trade-off between egg size and clutch size: eggs from smaller clutches tended to be larger (Fig. 2). Mean egg mass increased with maternal SVL when controlling for the effects of clutch size at Lerma ($\beta = 0.383$, $P = 0.012$) but not at El Pardo ($\beta = 0.073$, $P = 0.711$).

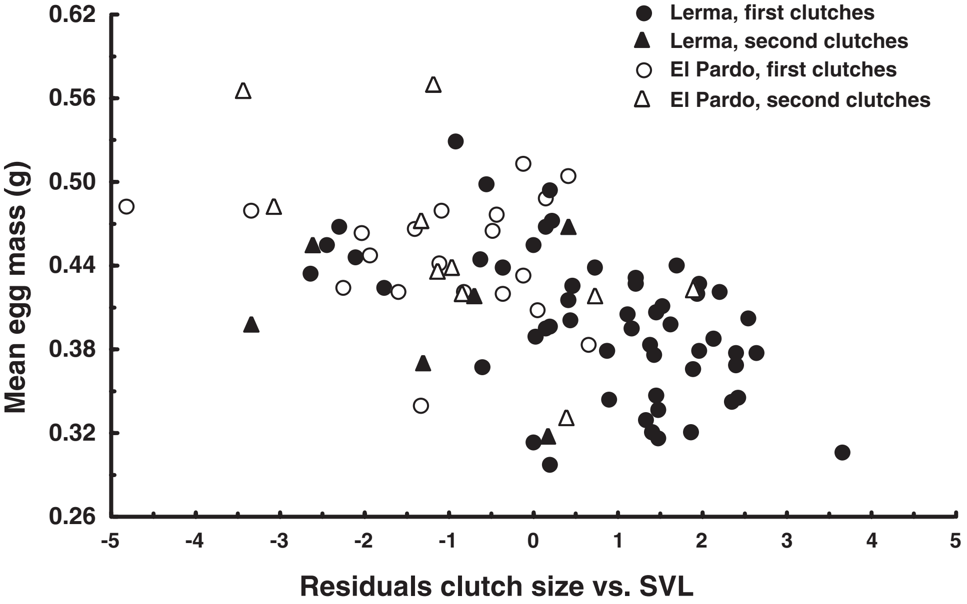

Figure 2. Trade-off between mean egg mass and relative fecundity (residuals of clutch size on snout–vent length; see text for details) for first and second clutches of northern (Lerma) and southern (El Pardo) females.

INCUBATION TIMES

In 2002, clutches from both populations were distributed evenly over two incubators set at a constant temperature of 30 ± 0.5 °C, and incubation times (which are strongly dependent on temperature) could be compared directly. Incubation was, on average, 6.3 days shorter for the clutches from Lerma (44.1 ± 0.2 days, $N = 34$) than for those from El Pardo (50.4 ± 0.6 days, $N = 12$); this population effect, which was highly significant ($F_{1,44} = 190.0$, $P < 0.0001$), accounted for 81% of the among-clutches variance in incubation times (Fig. 3). Although larger eggs had longer incubation times both between and within populations (ANCOVA with mean egg mass as the covariate, pooled within-cell regression: $\beta = 0.412$, $F_{1,42} = 8.6$, $P = 0.005$), the population effect remained highly significant when controlling for between-sites differences in mean egg size (ANCOVA, population effect: $F_{1,42} = 177.4$, $P < 0.0001$).

DISCUSSION

The results of the present study raise two main findings. First, although the overall reproductive investment was similar in both populations, there were differences in the distribution of that investment over the course of the reproductive season. Second, the northern, peripheral population showed a differentiated reproductive strategy along the clutch size versus egg size gradient: eggs were smaller, and first clutches were larger, than near the centre of the species' range.

REPRODUCTIVE INVESTMENT

The overall investment per reproductive season, indexed by the combined mass of first and second clutches, was similar in both populations, suggesting that the energy available to gravid females was not the main factor determining their reproductive strategies. Several lines of evidence support this conclusion. First, the SVL-adjusted postlaying body mass of females was similar in both populations. Second, although the energy available for second clutches was standardized for all years and populations because all animals were fed *ad libitum* in the laboratory, southern females laid second clutches more frequently than northern ones. Finally, neither clutch mass, nor clutch size showed significant among-year variation, despite apparent differences in precipitation, which is a main cue of productivity for many species of oviparous lizards (Patterson, 1991; Anderson, 1994; Jordan & Snell, 2002).

However, the existence of an egg size/number trade-off has sometimes been interpreted as an indication that the proximate constraint on total investment is resource-based (Olsson & Shine, 1997a). An alternative explanation is that female body size and shape set limits to clutch size, egg size or both (Vitt & Congdon, 1978; Congdon & Gibbons, 1987; Shine, 1992; Du, Ji & Shine, 2005). Our data favour the latter interpretation because, in both populations, clutch mass and clutch size were positively correlated with female SVL, and larger females (whose body volume increases allometrically with SVL) laid larger clutches without reducing

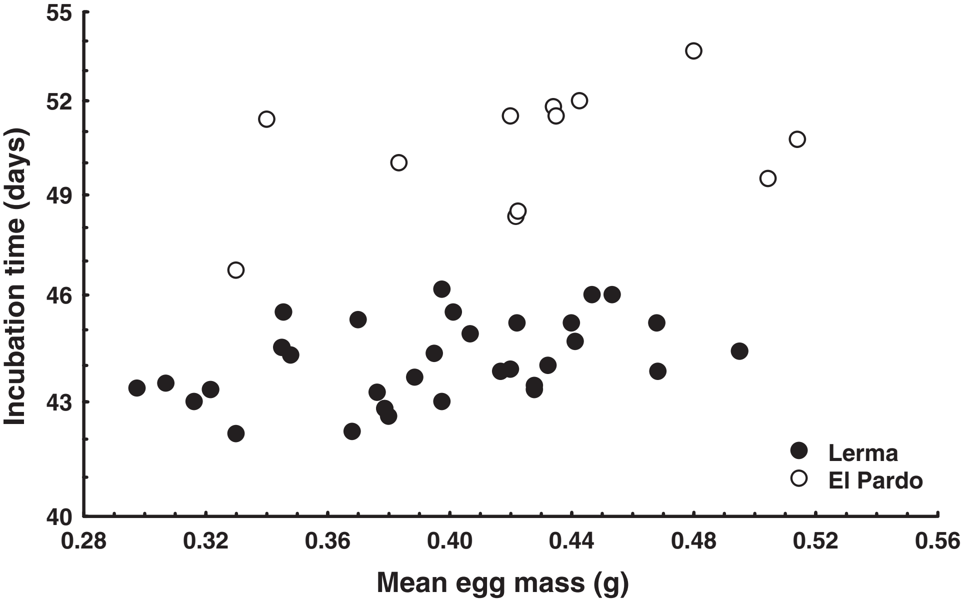

Figure 3. Mean incubation time as a function of mean egg size for clutches of northern (Lerma) and southern (El Pardo) females distributed evenly over two incubators set at a constant temperature of 30 ± 0.5 °C.

egg size (i.e. per offspring investment) to the extent that would have been expected on the basis of a resource-limited trade-off (Olsson & Shine, 1997a). Female size and mean egg mass were positively correlated, at least in the northern population, when controlling for the effects of clutch size. This result confirms that energy availability is not limiting reproductive investment at the northern edge of the species' range.

The between-populations difference in incubation times, with eggs from the northern population hatching approximately 1 week earlier at 30 °C, was among the clearest results of this study. Lizard incubation times seem genetically based and only partially dependent on egg size, as deduced from hybridization studies (Olsson *et al.*, 1996) and experimental manipulations of egg size (Sinervo, 1990). Our results are consistent with this view because the shorter incubation times of northern eggs were not attributable to their smaller size. If field incubation temperatures are lower at Lerma (a not unreasonable assumption), then the shorter incubation times of Lerma eggs may compensate for the longer development period due to the lower nest temperatures. Field observations indicate that the first hatchlings usually emerge during the first week of August at both study sites.

Northern females laid mostly first clutches composed of many eggs with relatively short incubation times, suggesting that hatching early is especially advantageous at the northern limit of the species'range. Previous studies have emphasized the relationship between that advantage and the substantial fitness penalty of late offspring in environments where summers are brief, and the time available for incubation and subsequent growth prior to winter is severely limited (Olsson & Shine, 1997b). Nevertheless, an alternative explanation could be that early juveniles at the northern limit of their Mediterranean range may have the opportunity to grow rapidly before their first winter. However, in more southern, drier habitats (such as El Pardo), food scarcity may penalize older and bigger juveniles with relatively higher energy demands. We have data that support this interpretation, which demonstrate that, after controlling for familial effects and egg incubation environment, hatchlings grew more slowly at El Pardo, and had a worse body condition, than at a nearby montane forest with higher food availability (Iraeta *et al.*, 2006). Thus, early hatching would allow Lerma juveniles to grow faster than those from El Pardo despite their less favourable thermal conditions.

TRADE-OFF BETWEEN EGG SIZE AND CLUTCH SIZE

The second interesting finding concerned the partitioning of reproductive investment along the clutch size versus egg size continuum. Life-history theory predicts that, in environments where juveniles suffer from higher mortality rates, more but smaller offspring should be produced (Sinervo, Svensson & Comendant, 2000). Alternatively, because differences in egg size translate directly into differences in hatchling size (Sinervo, 1990; present study), offspring size should increase and clutch size should decrease in environments with an accentuated survival advantage of large juveniles (Sinervo, 1990; Sinervo *et al.*, 1992; Stearns, 1992; Svensson & Sinervo, 2000). It is difficult to test these ideas in the absence of data for size dependent mortality in each population, but we can offer some hypotheses. In Lerma, a previous study showed that offspring size appeared to influence survivorship of laboratory-reared juveniles released into the wild because larger egg and hatchling mass increased their probability of recapture during the following activity season (Díaz *et al.*, 2005). Overall, juvenile survivorship was low (15.7%), so that selection should favour high fecundity. On the other hand, the fitness penalty of too small offspring, combined with the egg size versus clutch size trade-off, should lead to optimizing selection on these traits (Sinervo *et al.*, 1992). The larger Lerma females produced not only larger clutches, but also relatively larger eggs, as shown by the positive partial correlation between mean egg mass and female size when controlling for the effects of clutch size. The large clutches of Lerma females also may be the result of selection maximizing maternal rather than offspring fitness (Einum & Fleming, 2000), if the clutch size maximizing the number of surviving offspring per female is associated with a mean egg mass causing a low probability of juvenile survivorship.

With respect to the putative survival advantage of large juveniles at El Pardo, the following hypotheses are plausible: (1) because the activity season is longer at the southern locality (with an average of 20% more sunshine hours between March and September), exposure to predators should be higher (Adolph & Porter, 1993), enhancing the competitive advantage of large sized juveniles (Ferguson & Fox, 1984); (2) because clutch mass depends primarily on clutch size, rather than mean egg mass, longer activity and subsequent higher predation risk could also penalize southern females burdened with large clutches due to locomotor impairment (Sinervo, Hedges & Adolph, 1991; Olsson, Shine & Wapstra, 2001), which could select for smaller clutches of larger eggs; and (3) the higher population densities at El Pardo could increase the competitive advantage of larger juveniles (Sinervo *et al.*, 2000; Svensson & Sinervo, 2000). Alternatively, resource limitation in late summer, a common circumstance in lowland Mediterranean environments, could promote selection for bigger hatchlings to compensate for reduced growth rate and to allow drought-induced low activity levels (Iraeta *et al.*, 2006). This would be consistent with previous studies that suggested an increase in the survival advantage of large offspring under conditions of food shortage (Ferguson & Fox, 1984) or in drought years (Sinervo *et al.*, 1992).

CONCLUSIONS

Although a reciprocal transplant experiment would be necessary to confirm the superior performance of each population in its own locality, our 'common garden' approach strongly suggests that both populations are well adapted to their respective environments, and that their life-history patterns presumably reflect genetic differences. This conclusion is also supported by the convergence of our results with those reported by Sinervo (1990) for the distantly related sceloporine lizard *Sceloporus occidentalis* along a much longer latitudinal gradient in western North America: the northern population had larger clutches, smaller eggs, and shorter incubation times. Nevertheless, other studies have emphasized that lizard life histories are phenotypically plastic, and that temperature, by affecting activity times, can also lead to a negative correlation between survival rate and fecundity among populations in different thermal environments (Adolph & Porter, 1993). However, physiological models would not predict higher clutch mass and clutch size at the locality with shorter potential activity time, as is the case in our northern population.

Thus, the life-history traits studied show enough variation, presumably of an adaptive nature, to cope with environmental challenges at the edge of the species' range. This does not necessarily mean that the degree of local adaptation is equal for both populations. If, however, the potential for variation is large, local adaptation processes may be widespread, favouring the wide altitudinal range of these lizards (from the sea level up to 2500 m in the Moroccan Atlas) and their recent expansion along the Pyrenean valleys (Bauwens *et al.*, 1986). Life-history variation and local adaptation may also be crucial for the long-term persistence of the species, especially in the current context of global change.

The traits studied appeared to be well adapted to local environmental conditions at the edge of the range, and we conclude that other factors must be invoked to explain the location and shape of range boundaries. One such factor might be the inability of females or embryos to undergo longer egg retention (Shine, 2005), combined with a scarcity of nest sites that are thermally and hydrically suitable for prolonged egg development further north (Strijbosch & Creemers, 1988; Shine, Elphick & Barrott, 2003). In summary, we encourage future studies that focus on the factors and processes explaining the range boundaries not only of northern lacertids such as *Zootoca vivipara* or *Lacerta agilis* (Olsson & Shine, 1997b), but also of Mediterranean species, by far the most abundant and with the most intriguing northern limits.

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