# Exploring female reproductive tactics: trade-offs between clutch size, egg mass and newborn size in lacertid lizards

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The persistence of populations is based on the optimization of reproductive processes as a means of compensating for the loss of individuals through mortality. One way of reaching this equilibrium is the coadaptation of reproductive traits defining different strategies. I explored these tactics in lacertid lizards by analysing the covariation between, on the one hand, clutch size and frequency, and on the other, egg mass, using independent contrast data from 42 species. In addition, I examined the influence of female and newborn size on these variables. All the traits investigated, with the exception of clutch frequency, are influenced by female body size, reflecting physical constraints on reproductive output. The negative trade-off between clutch size and newborn size on one hand and egg mass on the other is congruent with the partitioning of energetic resources to produce a few large or numerous small descendents. Clutch frequency is unrelated to the other female reproductive traits.

*Key words:* clutch frequency, clutch size, comparative method, egg mass, reproduction

## INTRODUCTION

Life-history theory predicts that fecundity and demographic traits interact with species survival, thereby defining a set of coadapted characteristics that produce reproductive tactics (Roff, 1992). Thus, reproductive strategies can be defined by measuring just a few variables such as clutch size, egg mass, clutch frequency, age and size at maturity. The analysis of patterns of covariation in these life-history traits within reptiles reveals the importance of body size and phylogeny, a fact attributable to physiological and anatomical constraints (Dunham & Miles, 1985). Analyses of allometric relationships between these variables in lizard species have typically shown a slow–fast gradient (Dunham & Miles, 1985; Stearns, 1984). "Fast" species are smaller and short lived, mature early and produce small clutches of relatively large eggs at short intervals. In contrast, "slow" species are bigger and long lived, exhibit delayed sexual maturity and generally produce one large annual clutch of comparatively small eggs.

Lacertid lizards exhibit a diversity of life-history tactics that matches this pattern. Bauwens & Díaz-Uriarte (1997) examined the pattern of covariation between body size, age at maturity and reproductive characteristics in a set of 18 Eurosiberian lacertids. In den Bosch & Bout (1998) analysed covariation between clutch traits in 64 European lacertids using conventional statistics. Recent advances in lacertid phylogenetics and progress in the knowledge of their reproductive biology offer the opportunity to explore patterns of covariation and compare them with previously conducted studies in lacertids.

I performed an analysis of the female reproductive traits of 42 lacertid lizards using comparative methods in order to answer the following questions: 1) how do reproductive variables covary, 2) does female body size have any effect on these variables, and 3) is there any interspecific trade-off between egg mass and clutch size?

## MATERIALS AND METHODS

I gathered reproductive data on 42 oviparous species of lacertid lizards from different bibliographical sources (Table 1). I considered *Psammodromus hispanicus edwardsianus* to be a distinct taxon because it is genetically highly differentiated from the nominal subspecies (S. Carranza, pers. comm.). Data for mean, minimum and maximum female snout–vent length (SVL), minimum newborn SVL, mean clutch size and individual egg mass were compiled. The maximum number of clutches laid by females during their annual activity was also recorded. In a few cases some data were taken directly from graphs since not all authors provide the corresponding statistics. All variables were log10-transformed prior to analysis.

Most biological traits evolve across the phylogenetic relationships of species and therefore cannot be considered to provide strictly independent data, a violation of one of the main assumptions of statistical analysis. The aim of calculating independent contrasts is to obtain phylogenetic data that can be used as input for conventional statistics (Felsenstein, 1985). I obtained independent contrasts of the log-transformed variables from PDTREE (Garland et al., 1993) by using a phylogenetic tree that combined the results of various morphologic and genetic studies (Fig. 1; Arnold 1998; Arnold et al., 2007; Fu, 2000). Branch lengths were estimated by maximum likelihood optimization from an aligned dataset of 664 nucleotides of 12s rRNA and cytochrome b, using the molecular clock option of PUZZLE (Schmidt & von Haeseler, 2003). Because these data are not available for *Heliobolus lugubris*, I used the homologous sequences for *H. spekii* (accession numbers may be obtained from the author on request). Following recent works on lacertid ecomorphology (Vanhooydonck & Van Damme, 2003), I considered the unresolved nodes of the phylogeny as hard polytomies, representing real explosive speciation events. In order to check the correct
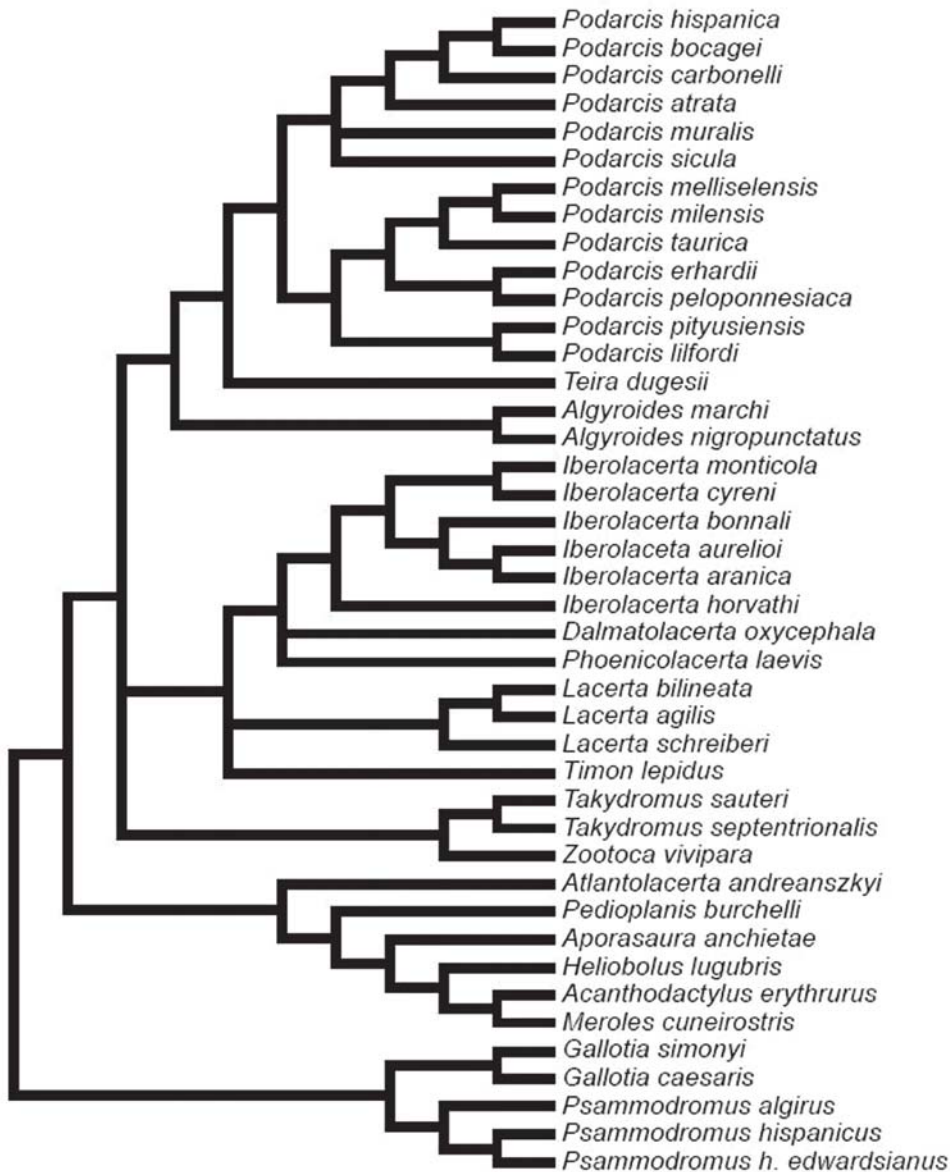
**Table 1.** Main reproductive traits of the 42 species of lacertid lizards used in this study: Min SVL – minimum juvenile SVL; Mean CS – mean clutch size; Mean EM – mean egg mass of individual eggs; CF – maximum clutch frequency per annual activity period.

| Species | Min SVL | Mean SVL | Mean CS | Mean EM | CF | References |
|---|---|---|---|---|---|---|
| *Podarcis hispanica* | 22.0 | 52.0 | 2.8 | 0.244 | 3 | Galán, 2003; Galán-Regalado, 2003 |
| *Podarcis carbonelli* | | 48.1 | 2.2 | | 1 | Pérez-Mellado, 1982 |
| *Podarcis bocagei* | 23.6 | 55.1 | 4.1 | 0.283 | 2 | Galán, 1996; Galán, 1999 |
| *Podarcis melisellensis* | | 63.1 | 4.3 | 0.263 | 3 | Bejakovic et al., 1995; Bejakovic et al., 1996a |
| *Podarcis lilfordi* | 29.0 | 61.9 | 2.5 | 0.630 | 2 | Castilla & Bauwens, 2000b |
| *Podarcis muralis* | | 67.9 | 5.5 | 0.277 | 1 | Bejakovic et al., 1996a,b |
| *Podarcis taurica* | | 63.6 | 3.8 | | 2 | Chondropoulos & Lyrakis, 1983 |
| *Podarcis pityusiensis* | 27.8 | 57.5 | 2.3 | | 1 | Carretero et al., 1995 |
| *Podarcis milensis* | 24.0 | 50.4 | 1.7 | | 2 | Adamopoulou & Valakos, 2002 |
| *Podarcis peloponnesiaca* | | 69.5 | 3.5 | | 2 | Maragou et al., 1999 |
| *Podarcis erhardii* | | 59.1 | 2.6 | | 2 | Maragou et al., 1999 |
| *Podarcis sicula* | | 66.3 | 4.6 | | 2 | Henle, 1988 |
| *Podarcis atrata* | 28.2 | 63.1 | 2.8 | 0.370 | 4 | Castilla & Bauwens, 2000a; Castilla et al., 1987 |
| *Teira dugesii* | 29.1 | 60.8 | 2.4 | 0.658 | 2 | Galán & Vicente, 2003 |
| *Lacerta bilineata* | | 109.5 | 13.2 | 0.950 | 1 | Braña, 1983; Braña et al., 1991 |
| *Lacerta agilis* | 29.0 | 85.0 | 9.2 | 0.599 | 1 | Amat, 1997; Amat et al., 2000 |
| *Lacerta schreiberi* | 27.0 | 108.4 | 13.7 | 0.716 | 1 | Marco et al., 1994; Marco, 1995 |
| *Timon lepidus* | 37.6 | 137.2 | 10.5 | 2.101 | 1 | Galán-Regalado, 2003 |
| *Iberolacerta aurelioi* | 26.4 | 55.3 | 2.5 | 0.430 | 1 | Arribas & Galán, 2005 |
| *Iberolacerta bonnali* | 23.6 | 56.2 | 3.0 | 0.460 | 1 | Arribas & Galán, 2005 |
| *Iberolacerta aranica* | 22.1 | 56.9 | 3.4 | 0.460 | 1 | Arribas & Galán, 2005 |
| *Iberolacerta monticola* | 22.9 | 64.4 | 6.4 | 0.417 | 1 | Rua & Galán, 2003 |
| *Iberolacerta cyreni* | 24.9 | 70.1 | 6.5 | 0.450 | 1 | Elvira & Vigal, 1985 |
| *Iberolacerta horvathi* | 24.5 | 56.8 | 3.7 | | 1 | Lapini et al., 1993 |
| *Dalmatolacerta oxycephala* | | 62.9 | 3.4 | 0.290 | 2 | Bejakovic et al., 1996a |
| *Phoenicolacerta laevis* | | 69.0 | 6.1 | | 3 | Hraoui-Bloquet, 1985 |
| *Algyroides marchi* | | 44.5 | 2.2 | | 1 | Rubio & Palacios, 1986; Palacios et al., 1974 |
| *Algyroides nigropunctatus* | | 56.7 | 3.3 | | 2 | Bejakovic et al., 1996a |
| *Zootoca vivipara* | | 55.5 | 6.5 | 0.240 | 1 | Braña et al., 1991 |
| *Takydromus septentrionalis* | | 65.0 | 3.1 | | | Ji et al., 1998 |
| *Takydromus sauteri* | | 67.0 | 2.0 | | 2 | Huang, 2006 |
| *Meroles cuneirostris* | | 49.0 | 2.9 | | 2 | Goldberg & Robinson, 1979 |
| *Acanthodactylus erythurus* | 31.3 | 71.0 | 3.6 | 0.820 | 2 | Castilla et al., 1992; Bauwens & Diaz-Uriarte, 1997 |
| *Pedioplanis burchelli* | | 54.1 | 4.5 | | 2 | Nkosi et al., 2004 |
| *Heliobolus lugubris* | 18.0 | 57.5 | 3.4 | | 2 | Goldberg, 2006 |
| *Aporosaura anchietae* | | 47.0 | 1.3 | | 4 | Goldberg & Robinson, 1979 |
| *Atlantolacerta andreanszkyi* | | 48.8 | 2.1 | | 2 | Busack, 1987 |
| *Psammodromus hispanicus* | | 42.2 | 3.6 | 0.256 | 2 | Pascual González & Pérez-Mellado, 1989 |
| *Psammodromus h. edwardsianus* | 21.4 | 42.7 | 2.9 | | 2 | Carretero & Llorente, 1991 |
| *Psammodromus algirus* | | 60.5 | 5.0 | | 2 | Carretero & Llorente, 1997 |
| *Galloria caesaris* | | 67.6 | 2.5 | 1.210 | 2 | García-Márquez et al., 1999 |
| *Gallotia simonyi* | | 143.8 | 11.7 | 5.200 | 2 | Rodríguez-Dominguez & Molina-Borja, 1998 |

calculation of the independent contrasts, I correlated their absolute values with their standard deviations.

I analysed the relationships between variables using the Pearson product-moment correlation coefficient. Bivariate allometries were investigated by means of the regression of independent contrasts forced through the origin and estimation of the slope of the ordinary least square (OLS) regression. In addition, to examine trade-offs between a pair of variables both influenced by a third variable, I performed an OLS regression through the origin of independent contrasts of each variable on this third variable. I then calculated the Pearson correlation between the residuals of each OLS regression. The use of partial regression coefficients has the disadvantage of

**Fig. 1.** Molecular phylogenetic tree depicting the evolutionary relationships between the lacertids analysed in this study.

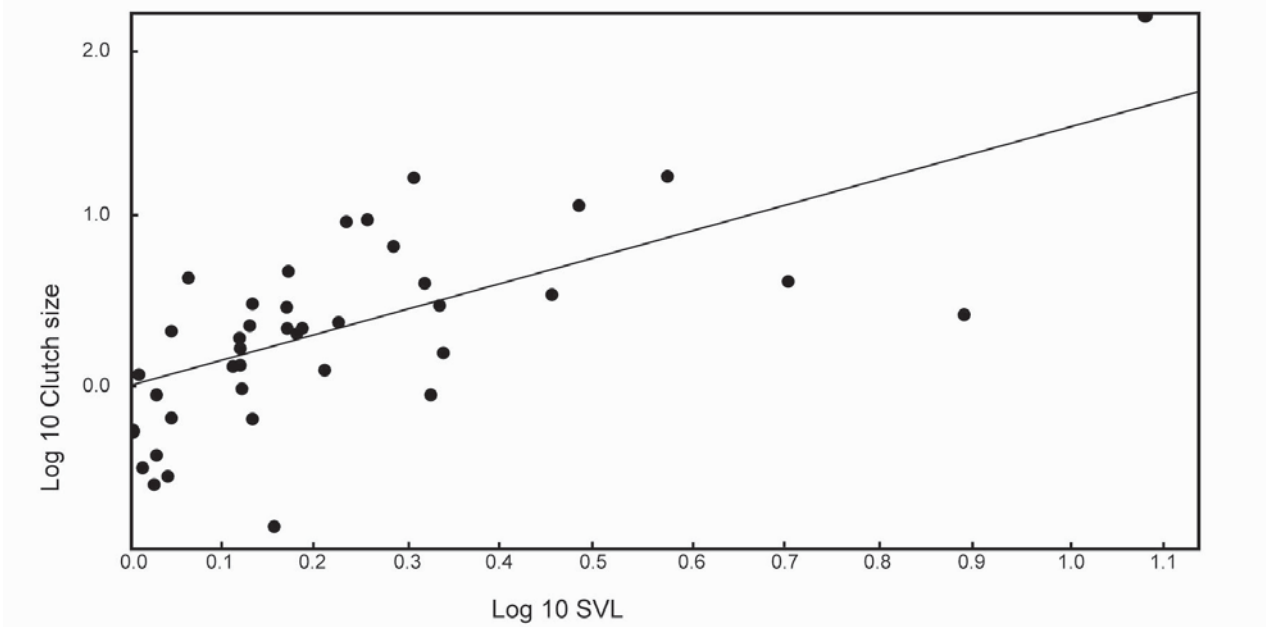suffering from biased estimates when the independent variables are highly correlated (Slinker & Glantz, 1985).

## RESULTS

None of the correlations between the absolute values of the independent contrasts and their standard deviations were significant and so they can be considered as statistically independent values.

The minimum SVL of newborns and SVL at sexual maturity are strongly correlated with the maximum SVL ($r=0.6052$, $P=0.0030$, $n=18$ and $r=0.9764$, $P<0.01$, $n=39$). Thus, large species mature at larger body sizes and have larger offspring. Mean clutch size increases significantly with mean female SVL ($r=0.7645$, $P<0.0001$, $n=41$; Fig. 2). I found covariation between mean values of egg mass and clutch size, and both variables are positively and significantly correlated ($r=0.4998$, $P<0.0089$, $n=21$). Nevertheless, the increase in female SVL produces a sig-

nificant increase in mean egg mass ($r=0.8806$, $P<0.0001$, $n=21$) and clutch size, thereby confounding the relationships between those variables. Therefore, I performed an OLS regression of mean clutch size and egg mass on mean female SVL to obtain their residual variation as a measure of relative clutch size and egg mass. As a result, I found a negative and significant trade-off between both relative measures of egg mass and clutch size ($r=-0.4477$, $P=0.0042$, $n=21$; Fig. 3). Mean egg mass was significantly and positively correlated with the minimum SVL of newborns ($r=0.7098$, $P=0.0461$, $n=13$). Moreover, there was a significant negative correlation between relative clutch size and the relative minimum size of newborns ($r=-0.5198$, $P=0.0470$, $n=15$, Fig. 4). Thus, species with a lower relative clutch size produce comparatively larger offspring than expected given their maternal body size.

Mean female SVL is not correlated with the maximum number of clutches laid per annual period of activity ($r=-0.0076$, $P=0.0843$, $n=40$). Moreover, both absolute

**Fig. 2.** Plot of independent positivized contrasts from log-transformed means of female SVL and clutch size (slope = 1.551).
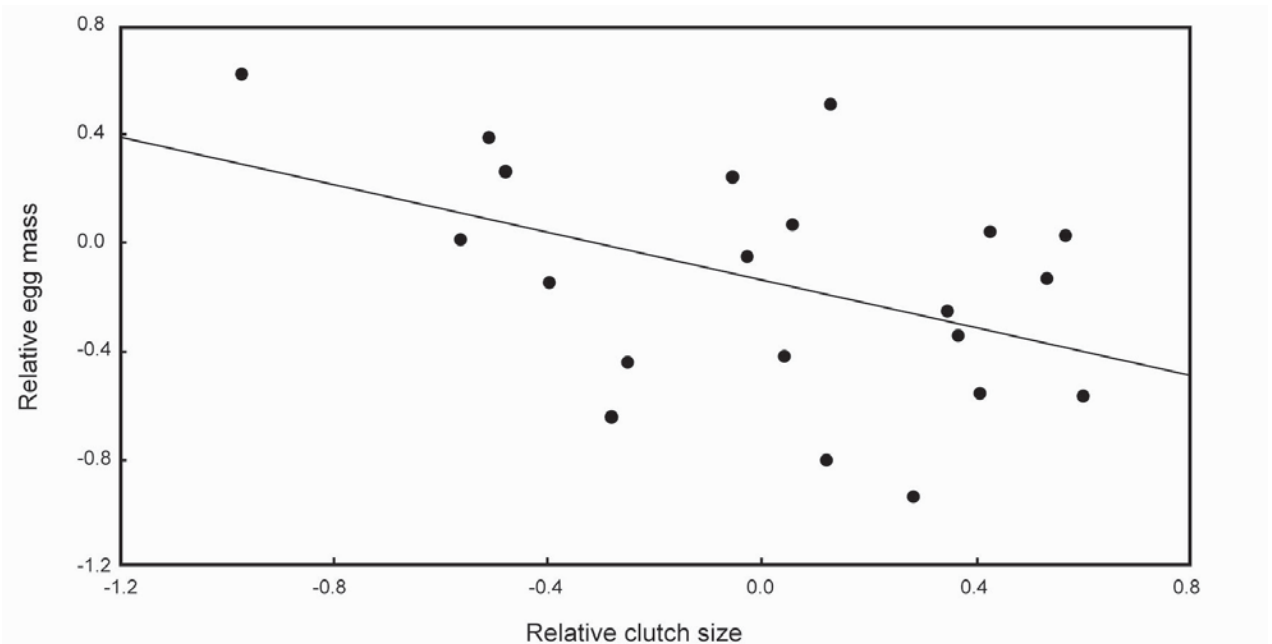
mean clutch size and egg mass are independent of maximum clutch frequency ($r=-0.1315$, $P=0.2061$, $n=40$ and $r=-0.0374$, $P=0.4342$, $n=21$).
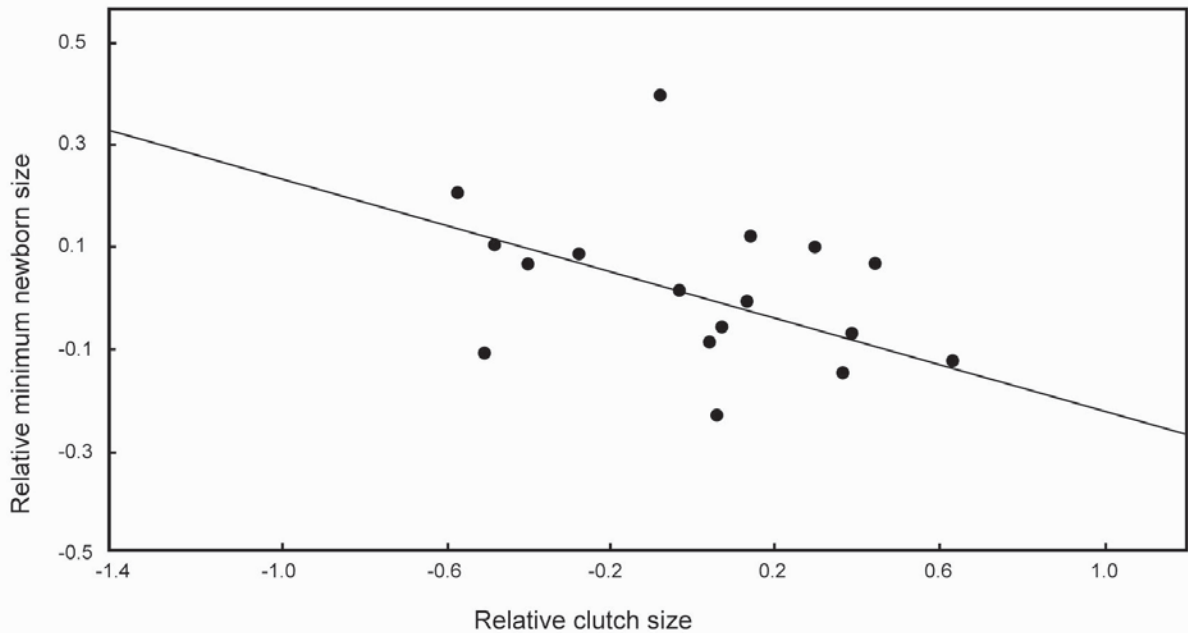
## DISCUSSION

Comparative analysis of life-history traits in 42 lacertid lizards reveals a complex strategy based on three different components: 1) the physical constraints of body size on clutch size and egg mass; 2) a trade-off between clutch size and egg mass on one hand, and newborn size on the other; and 3) the independence of body size and the trade-off with clutch frequency.

Body size and shape have a crucial importance for fecundity in reptiles as they constrain the energy allocated to reproduction. Bigger species may potentially accumulate larger fat reserves in their abdominal cavity and so be able to produce numerous eggs per clutch. At the intraspecific level, energy availability determines effective fecundity with respect to potential fecundity predicted by maternal body size (Olsson & Shine, 1997). Also at the intraspecific level temporal or individual dif-



**Fig. 3.** Negative allometry between relative egg mass and relative clutch size estimated as residuals of the regression of clutch size and egg mass on mean SVL (slope = −0.4476).

**Fig. 4.** Negative allometry between relative newborn size and relative clutch size estimated as residuals of the regression of clutch size and egg mass on mean SVL (slope = –0.4732).

ferences in the ability to use resources disappear and a limiting effect of body size on fecundity emerges. Accordingly, numerous studies report a correlation between clutch mass or size and female body size or shape in lacertids and other reptiles (Bauwens & Díaz-Uriarte, 1997; Dunham and Miles, 1985; In den Bosch & Bout, 1998; Griffith, 1994; Kratochvíl & Kubička, 2007; Thompson & Pianka, 2001).

Clutch size and egg mass provide a measurement of fecundity and energetic expenditure per descendent or, in other words, the quantity and quality of the investment in energetic terms for a given reproductive output. A negative trade-off between clutch size and egg mass after controlling for the influence of body size has been detected in interspecific (Castilla & Bauwens, 2000a,b) and intraspecific studies (Bauwens & Díaz-Uriarte, 1997; In den Bosch & Bout, 1998). In addition, there is also a negative trade-off between clutch size and newborn size when the influence of maternal size is eliminated in statistical analyses. Such trade-offs are probably the most remarkable aspect of female reproductive tactics in lacertids. Larger species produce numerous clutches of proportionally smaller eggs and give birth to relatively smaller offspring. On the other hand, smaller species are characterized by clutches of few but comparatively large eggs and large newborns (Bauwens & Díaz-Uriarte, 1997). Smaller species compensate for their low number of descendents by producing relatively large offspring that mature more quickly. Thus, in relative terms, larger lacertids invest more energy in fecundity than smaller species, which invest more energetic resources in the quality of their descendents than in their number.

As in other studies of lacertids (Bauwens & Díaz-Uriarte, 1997), I found no influence of female body size on clutch frequency. Lacertid lizards inhabit a wide variety of climates that constrain their annual activity and hence their annual number of clutches in different manners. In Mediterranean or temperate climates small *Podarcis* and *Takydromus* produce up to four clutches per year, unlike larger lacertids such as *Timon* and *Lacerta*. Lizards inhabiting higher altitudes (for example, the genus *Iberolacerta*) lay only one annual clutch and larger lizards are unable to colonize these environments and compete. Several studies have analysed each clutch season in multiple layers (Castilla & Bauwens, 2000a,b; Galán-Regalado, 2003; Ji et al., 2007) and suggest that for each layer there is a trade-off between clutch size and egg mass. Thus, species can adjust their reproductive output to temporal variation in predatory pressures and resource availability.

## ACKNOWLEDGEMENTS

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