



A comparative study of clutch size, range size, and the conservation status of island vs. mainland lacertid lizards

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ABSTRACT

Whereas the range size of endangered species is undoubtedly useful to predict risk of extinction, the role of their life-history characteristics is much less clear, and their effects may depend on the nature of the threatening factors. Such factors, for instance, are known to be different on islands and on the mainland. We used phylogenetically based statistical analyses to study the relationships among conservation status, insularity, range size, and life-history traits in a clade of Western Palearctic lacertids including insular and continental species. These lizards are ecologically similar, but they show wide variation in life-history traits and vulnerability to extinction. Insular species of a given size had smaller clutches than mainland ones. Degree of threat was best predicted by a logistic regression including range size, insularity, clutch size, and the insularity \times clutch size interaction. On the mainland, but not on islands, threatened species had smaller clutches than non-threatened ones. On islands, small clutch size is probably an adaptive trait, and it might predispose certain species to extinction, but the intrinsic characteristics of such species remain unclear. However, small clutch size was a good predictor of extinction risk on the mainland, having evolved most frequently in late maturing species from montane habitats in which climatic conditions limit their reproductive output and increase their vulnerability to stochastic hazards or habitat fragmentation.

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1. Introduction

With increased concern about biodiversity losses (Pimm et al., 1995), conservation biologists have sought general patterns in life-history traits that may render a species more or less prone to extinction. Both the areal extent of a species' distribution and the abundance of mature individuals, which play an apparent role in the IUCN Red List categories and criteria, are undoubtedly useful, along with population tendency over time, to predict risk of extinction (O'Grady et al., 2004). However, these criteria do not always take into account the life histories of the taxa under consideration, which leads to situations in which the risk of extinction may be under- or over-estimated (Mattila et al., 2008). Ecological theory predicts that extinction risk should be higher in species with low rates of population increase, large fluctuations in the number of individuals, and/or short lifespans (Pimm et al., 1988). Other studies have pointed out ecological specialization or low fecundity as the main traits related to greater extinction rates (Foufopoulos and Ives, 1999; Cardillo, 2003). However, several problems complicate the study of the associations between life-history characteristics and probability of extinction. For example, life-history traits are

frequently intercorrelated to a large extent (Stearns, 1992; Bauwens and Díaz-Uriarte, 1997), which makes it difficult to sort out what factors are primarily responsible for an increased susceptibility to extinction. More importantly, species-specific life-history characteristics may be of limited utility to predict vulnerability to extinction in the current scenario of man-induced global change. Instead, other authors emphasize the prevalence of extrinsic, anthropogenic factors such as habitat loss, over-exploitation, or introduced predators or competitors in the extinction of contemporary species (Purvis et al., 2000). Still others underline the interaction between the intrinsic attributes that render certain species susceptible to extinction and the intensity and nature of the factors that threaten them (Purvis et al., 2005). This latter view offers the advantage that it allows life-history traits to influence extinction risk in complex ways that may vary between different ecological scenarios.

From that perspective, the comparison between mainland and island taxa has been a main focus of interest for evolutionary ecologists and conservation biologists (Foufopoulos and Ives, 1999; Manne et al., 1999; Knapp et al., 2006). Some of these studies have found that extinction risk is actually higher on the mainland than on islands when holding for the effects of range size (Manne et al., 1999). Others have shown that local abundances may be one order of magnitude higher on islands than on mainlands, but only due to reduced predation and competition which leads to an enhanced

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sensitivity of insular communities to extinction after the arrival of introduced predators or competitors (Buckley and Jetz, 2007). Extensive research with *Anolis* lizards in the Caribbean Islands (reviewed by Losos (1994)) has revealed that low levels of predation and interspecific competition may lead to high densities, high intraspecific competition, and in some cases narrow, specialized niches; narrow-niche species are more sensitive to any sort of environmental change, and have a higher potential for extinction (Cardillo, 2003; Boyles and Storm, 2007).

Within this context, our aim is to employ phylogenetically based statistical analyses (Felsenstein, 1985; Garland et al., 1993) to study the relationships among conservation status, range size, and clutch size adjusted for body size (snout-vent length, SVL) in lacertid lizards from the Iberian peninsula and the Balearic and Canarian archipelagos. These lizards have several important advantages as a model system. Firstly, low energy requirements and behavioural thermoregulation allow vast variation in their life-history traits via phenotypic plasticity or adaptation to local environments (Shine, 2005). Secondly, they combine such variation with similar body shape, reproductive mode, diurnal activity patterns, and thermoregulatory behaviour (Arnold, 1987; Bauwens et al., 1995). Thus, our choice of species should minimize the risk that patterns of association are masked or induced by traits not included in our analyses (Bauwens and Díaz-Uriarte, 1997). Thirdly, the conservation status of these lizards ranges from species that are extremely abundant to closely related taxa that are among the most critically endangered lizard species on earth. For instance, *Gallotia galloti* from Tenerife can be regarded as an agricultural pest, whereas *Gallotia bravoana*, the giant lizard from La Gomera, occupies an area of less than 2 ha and has a wild population of about 100 individuals (Pleguezuelos et al., 2002).

The specific questions we seek to answer are: (1) is the SVL-adjusted clutch size of lacertid lizards a good predictor of extinction risk? Is it correlated with the biogeographical criteria employed by the IUCN to define threat categories?; (2) If positive, how are these relationships affected by insularity? Are all types of traits equally effective for predicting extinction risk in insular and continental species?; and (3) To what extent are these relationships confounded by phylogenetic effects? To answer these questions, we used phylogenetic Generalized Linear Models as an extension of the Monte Carlo method initially designed by Garland et al. (1993) to perform phylogenetic analyses of (co)variance by computer simulation.

2. Material and methods

2.1. Data

Our choice of species and literature sources were guided by the following criteria: firstly, to work with homogeneous databases, thus avoiding inconsistencies due to differences in risk assessment between global and regional scales (Gardenfors, 2001); secondly, to cover a regional yet sufficiently contrasted biogeographical scale that allows a direct association between the scales of measurement of biogeographical and life-history variables; and thirdly, to include as many species with reliable data for the variables of interest as possible. For that purpose, we used the lacertid species in the revised edition of the Checklist of the Amphibians and Reptiles of Spain (Montori and Llorente, 2005). From the 33 species in that list, we excluded the three introduced ones (*Lacerta perspicillata*, *L. tangitana* and *Podarcis sicula*) plus two former subspecies which have achieved specific status only recently and lack reliable data for the variables considered in this study (*Podarcis vaucheri* and *Iberolacerta martinezricai*). On the other hand, we included *I. monticola*

instead of the nominal subspecies *I. monticola monticola* because of its well characterized disjunct distribution range and the accessibility of biogeographical and reproductive data. This produced a final data set of 27 species for which we gathered data about conservation status, insularity, size of the distribution range, altitudinal range, snout-vent length, and average clutch size. We obtained the conservation status from the most recent Red List of Spanish Amphibians and Reptiles (Pleguezuelos et al., 2002), and we regrouped the five IUCN status categories into two: non-threatened (Low concern or Near threatened) and threatened (vulnerable, endangered or critically endangered). This allowed us to avoid an excessive number of species-groups with too small sample sizes. Biogeographical variables were taken from Pleguezuelos et al. (2002) and Loureiro et al. (2008), and they included insularity (defined in a narrow sense, i.e. restricted to species which are confined to one or more oceanic islands), range size (number of 10×10 km² squares within the study area in which a species was recorded), and altitudinal range (which was negatively correlated with its lower limit, as an index of the biogeographical restriction of some species to montane habitats, but showed a much better distribution for statistical purposes). Data about body size (snout-vent length, SVL) and average clutch size were collected from the literature; they are available as electronic Supplementary material. Data are given as mean \pm 1 SE.

2.2. Analyses

We analysed relationships between variables using either General Linear Models (i.e. ANOVA, linear regressions, and ANCOVA) or logistic regressions with conservation status as the dependent, binomial variable. When necessary, we log-transformed variables to meet the requirements of parametric tests. We also considered the fact that species are part of a hierarchically structured phylogeny and cannot therefore be regarded as statistically independent data points, but must be examined with appropriate comparative methods (Felsenstein, 1985; Garland et al., 1993). The comparative methods of our choice were Felsenstein's (1985) phylogenetically independent contrasts (hereafter PICs) and the Monte Carlo method initially designed for phylogenetic analyses of (co)variance by Garland et al. (1993). We constructed our phylogenetic hypothesis (Fig. 1) combining different published sources, which report putative phylogenetic relationships of extant Lacertidae (Bauwens et al., 1995; Bauwens and Díaz-Uriarte, 1997; Hernández et al., 2001; Carranza et al., 2004; Arnold et al., 2007). Branch lengths, which are needed to simulate the evolution of traits (Garland et al., 1993) and to standardize PICs (Felsenstein, 1985; Garland et al., 1992; Díaz-Uriarte and Garland, 1998) under a gradual Brownian motion model of evolutionary change (hereafter GBM), were modified from Bauwens et al. (1995) after having incorporated a few changes to accommodate the new information available. However, we also performed our analyses employing unit (i.e. constant) branch lengths, which is equivalent to assume a speciation model of evolution (speciation Brownian motion, hereafter SBM).

For the Monte Carlo simulations we used the *Phenotypic Diversity Analysis Programs* software package (PDAP's) developed by Garland et al. (1993). These authors proposed using empirically scaled computer simulation models of traits evolving along known trees to obtain null distributions of statistics. Nevertheless, since the non-phylogenetic analyses provide the values that are needed to calculate the 'phylogenetically correct' significances (by counting the number of statistics obtained in the simulations which exceed such values), we also present the conventional, phylogenetically uncorrected results. Moreover, results are frequently similar in phylogenetic and non-phylogenetic analyses, and the non-phylogenetic approach avoids the drawbacks of comparative methods

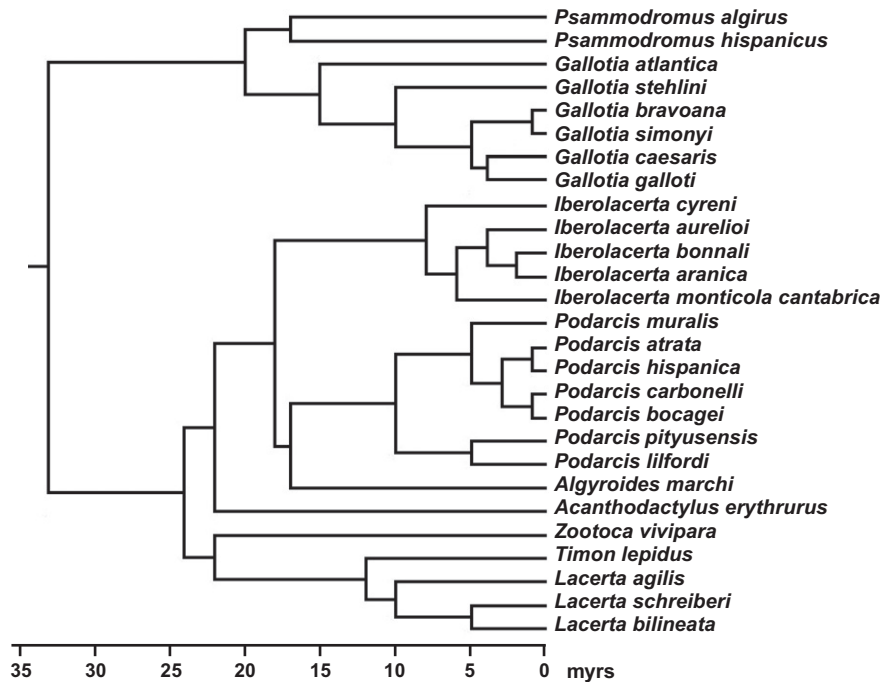


Fig. 1. Phylogenetic hypothesis used for comparative analyses, with branch lengths in millions of years. See text for details about the sources employed to build the phylogeny and to assign branch lengths.

when there is uncertainty about models of evolutionary change or phylogenetic topology (Price, 1997).

We used the program PDSIMUL from PDAP to create the simulated sets of random phenotypic data. To keep realistic phenotypic values for the simulated data we bounded the variables within the following limits: for clutch size, between 1 and 30 eggs (which is larger than the maximum values reported for *Timon lepidus*); for SVL, between 30 (which is less than the SVL of the smallest lacertid known, *Ophisops beddomei*) and 350 mm (which is between the maximum length of the largest species in our data set, and the maximum estimated length of the fossil giant lizard *Gallotia goliath*); for range size, between 0.4 and 6000 10×10 km² squares (which covers the whole extension of the Iberian peninsula plus the two archipelagos); and for altitudinal range, between 50 (which is below the 67 m altitude of the Columbretes Islands, which form the distribution range of the endemic species *Podarcis atrata*) and 3718 m (altitude of the highest peak, Teide, in the Canary Islands). We kept simulated trait values within the specified limits by using the REPLACE option of PDSIMUL. The seed for random numbers, determining which string of pseudo-random numbers the program uses, was 7. We used the between-species means of the real data as starting values and as the expected means of the generated tip values, and we set the expected variances of the simulated tip data equal to the variances of the real data. We set the correlations between the simulated changes for the two traits either equal to zero, except in the ANCOVAs of log-clutch size adjusted for log-SVL as a function of insularity, for which we also used a correlation equal to the actual value obtained with the real data. We used both the gradual (i.e. with variable branch lengths) and speciational (i.e. with all branch lengths set equal to one) Brownian motion models of evolutionary change.

We used the program PDANOVA from PDAP to create phylogenetically correct null distributions of ANCOVA statistics from 1000 sets of tip values generated by PDSIMUL. However, PDANOVA is restricted to perform one-way analyses of (co)variance. Hence, to test the phylogenetically-adjusted significance of predictors in logistic regressions, we employed batch files to read simulated data

sets into the Generalized Linear/Nonlinear Models (GLZs) module of Statistica version 9 (Hill and Lewicki, 2007). We used type III likelihood ratio tests to compute independent tests of the increment in the log-likelihood attributable to each effect, while controlling for all other effects in the model (Hill and Lewicki, 2007).

3. Results

Range size, altitudinal range, SVL-adjusted clutch size, and insularity (i.e. the potential predictors of conservation status) were intercorrelated to a large extent (Tables 1 and 2). Thus, body size and clutch size were positively correlated in our species set, following the general pattern found in lacertid lizards. Between-species variation in geographical range size was positively correlated with variation in altitudinal range. Interestingly, these two variables were also correlated with SVL-adjusted clutch size, showing that for a given body size widely distributed species tend to lay more eggs than narrowly distributed ones (Table 1). Insular species had smaller distribution ranges and narrower altitudinal ranges, and they were somewhat larger, than continental one (Table 2). However, all these differences lost significance in the phylogenetic analyses, probably because there were only three independent episodes for the evolution of insularity. SVL-adjusted clutch size was smaller in insular than in continental lacertids (Fig. 2) both in a conventional ANCOVA ($F_{1,24} = 32.78$ and $P < 0.001$ for insularity, $F_{1,24} = 95.85$ and $P < 0.001$ for log-SVL) and in phylogenetic ANCOVAs either with a correlation between the simulated changes for the two traits set equal to zero (GBM: $P = 0.003$ for insularity and $P < 0.001$ for log-SVL; SBM: $P = 0.001$ for insularity and $P < 0.001$ for log-SVL) or set equal to the 0.741 value obtained for the real data (GBM: $P < 0.001$ for insularity and $P = 0.090$ for log-SVL; SBM: $P = 0.001$ for insularity and $P = 0.069$ for log-SVL).

To explore what variables were more closely related to conservation status, while taking into account the relationships among them, we combined the traditional null hypothesis testing approach based on stepwise multiple regressions with inferences

Table 1
Pearson's correlations between log₁₀-body size (snout-vent length, SVL), log₁₀-clutch size, log₁₀-distribution range, and altitudinal range of 27 species of lacertid lizards. Values above the diagonal show conventional, non-phylogenetic analyses of tip-species data; values below the diagonal show values based on phylogenetically independent contrasts. GBM: contrasts assuming a gradual Brownian motion model of evolutionary change; SBM: contrasts assuming a speciation Brownian motion model of evolutionary change. SVL-adjusted clutch size: residuals of the corresponding regression of log₁₀-clutch size on log₁₀-SVL.

		Snout-vent length	Clutch size	Distribution range	Altitudinal range	SVL-adjusted clutch size
Snout-vent length		–	0.741 <i>P</i> < 0.001	–0.081 <i>P</i> = 0.686	0.0274 <i>P</i> = 0.892	–
Clutch size	GBM	0.603 <i>P</i> < 0.001	–	0.294 <i>P</i> = 0.137	0.324 <i>P</i> = 0.099	0.671 <i>P</i> < 0.001
	SBM	0.744 <i>P</i> < 0.001				
Distribution range	GBM	–0.043 <i>P</i> = 0.831	0.340 <i>P</i> = 0.083	–	0.790 <i>P</i> < 0.001	0.453 <i>P</i> = 0.018
	SBM	0.131 <i>P</i> = 0.514	0.337 <i>P</i> = 0.086			
Altitudinal range	GBM	0.011 <i>P</i> = 0.956	0.285 <i>P</i> = 0.149	0.943 <i>P</i> < 0.001	–	0.528 <i>P</i> = 0.005
	SBM	0.199 <i>P</i> = 0.553	0.361 <i>P</i> = 0.065	0.861 <i>P</i> < 0.001		
SVL-adjusted clutch size	GBM	–	0.817 <i>P</i> < 0.001	0.365 <i>P</i> = 0.061	0.457 <i>P</i> = 0.017	–
	SBM		0.703 <i>P</i> < 0.001	0.412 <i>P</i> = 0.033	0.364 <i>P</i> = 0.062	

Table 2
Mean (±1SE) values of body size, clutch size, distribution range, and altitudinal range for mainland (*N* = 18) and insular (*N* = 9) species of lacertid lizards. Results of ANOVAs, both conventional and phylogenetic, are also shown. Corrected *P*-values in phylogenetic ANOVAs are based on simulated data that 'evolve' along the phylogeny following a gradual (GBM) or speciation (SBM) Brownian motion model of evolutionary change.

	Mean ± 1SE		Conventional ANOVAs		Phylogenetic ANOVAs	
	Mainland species	Island species	<i>F</i> _{1,25}	<i>P</i>	<i>P</i> (GBM)	<i>P</i> (SBM)
Snout-vent length (mm)	70.9 ± 7.0	96.7 ± 15.2	3.40	0.077	0.423	0.362
Clutch size (no. of eggs)	5.93 ± 0.95	4.44 ± 0.98	1.30	0.266	0.612	0.580
Distribution range (no. of 10 × 10 km ² squares)	946.1 ± 335.5	21.3 ± 6.4	11.82	0.002	0.079	0.068
Altitudinal range (m)	1812 ± 166	942 ± 330	6.98	0.014	0.143	0.169

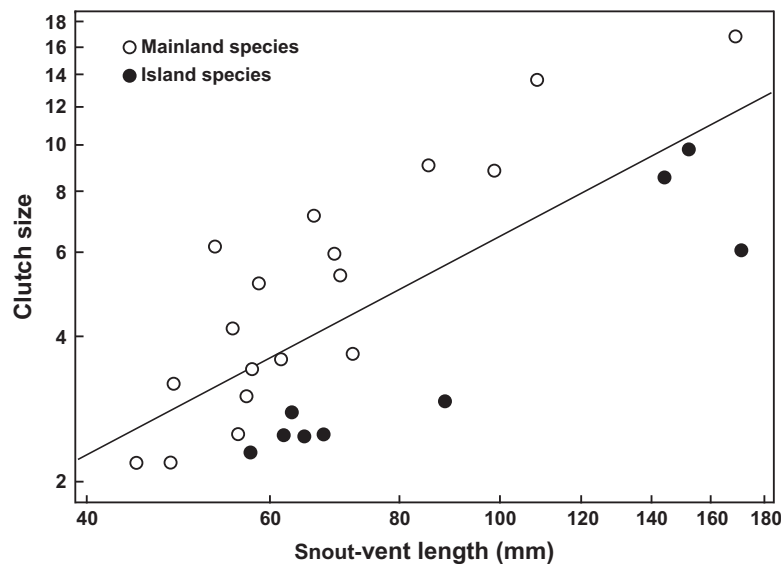


Fig. 2. Regression of clutch size on body size in mainland and island species of Iberobaleaic and Canarian lacertid lizards.

based on model selection using the Akaike information criterion. Firstly, we tested the full factorial models formed by each continuous predictor (range size, altitudinal range, and SVL-adjusted clutch size) plus insularity and the interaction between them (Models 1–3 in Table 3). Secondly, we tested the overall model including log-distribution range, insularity, SVL-adjusted clutch

size, and the interaction between insularity and SVL-adjusted clutch size (Model 4 in Table 3). Threatened species had smaller geographical range sizes than non-threatened ones both in conventional and phylogenetic analyses (logistic regression, Model 1 in Table 3). This is not unexpected, since this variable is actually employed for the definition of IUCN conservation categories.

Table 3

Logistic regression models (terms in the equation, coefficients in the linear predictor, type 3 log-likelihood ratios, chi-square values, and associated P -values) predicting the probability that a given species will be categorized as threatened (P_{threat}) or not ($1 - P_{threat}$) as a function of log-distribution range, altitudinal range, insularity (coded +1 for continental species and -1 for insular ones), SVL-adjusted clutch size (residuals of log-clutch size on log-SVL), and/or the interaction between insularity and SVL-adjusted clutch size. For each model, the percentage of correctly classified cases is shown in parentheses. Corrected P -values in phylogenetic GLZs are based on simulated data that 'evolve' along the phylogeny following a gradual (GBM) or speciation (SBM) Brownian motion model of evolutionary change.

Model	Predictors of $P_{threat} = 1/(1 + e^Z)$	Coefficients in Z	Conventional GLZs			Phylogenetic GLZs	
			Log-likelihood	χ^2 ($df = 1$)	P	P (GBM)	P (SBM)
#1 (81.5 %)	Intercept	-3.300	-17.80	14.96	<0.001	<0.001	0.001
	Log ₁₀ -distribution range	2.373					
#2 (88.9 %)	Intercept	-6.004	-17.64	22.31	<0.001	<0.001	<0.001
	Altitudinal range	0.626					
	Insularity	-2.773					
#3 (74.1 %)	Intercept	-0.065	-15.03	4.53	0.033	0.076	0.108
	SVL-adjusted clutch size	7.430					
	SVL-adjusted clutch size \times insularity	9.193					
#4 (92.6 %)	Intercept	-90.475	-5.64	7.17	0.007	0.014	0.011
	Insularity	-23.112					
	Log ₁₀ -distribution range	48.722					
	SVL-adjusted clutch size	138.943					
	SVL-adjusted clutch size \times insularity	178.682					

However, and contrary to expectations, the frequency of taxa classified according to conservation status did not differ between continental and insular species ($\chi^2 = 0.32$, $df = 1$, $P = 0.573$). Moreover, when controlling for the effects of altitudinal range (Model 2), probability of threat was larger for continental than for insular species (Table 3). Concerning the effects of SVL-adjusted clutch size on probability of threat (Model 3), these were significant only in non-phylogenetic analyses. However, there was a significant interaction between the effects of insularity and SVL-adjusted clutch size on conservation status both in conventional and in phylogenetic analyses, showing that threatened mainland species had lower clutch sizes for their SVL than non-threatened ones, whereas all island species had low clutch sizes for their body size independently of their conservation status (Fig. 3). Finally, when we considered the combined effects of insularity, geographical range size, and SVL-adjusted clutch size on conservation status, the best subsets approach to model selection produced a logistic regression (Model 4 and Fig. 3; Akaike $IC = 14.1$, log-likelihood = 31.49, $df = 4$, $P < 0.001$; Akaike IC for the next model = 17.60) in which probability of threat: (1) decreased with log-distribution range and SVL-

adjusted clutch size, although this latter effect was important only for continental species and (2) it was smaller for insular lacertids while controlling for the effects of all other variables in the equation (Table 3).

4. Discussion

Overall, our analyses show that the conservation status of the lacertids included in our sample was highly correlated not only with their range size and altitudinal range (which is not unexpected, since geographical range size is among the criteria employed to define conservation status), but also with a basic life-history trait such as SVL-adjusted clutch size. Previous studies have shown that low fecundity, of which low clutch size is an important component, can significantly increase the risk of extinction in amphibians (Hero et al., 2005), birds (Bennett and Owens, 1997), and mammals (Purvis et al., 2000; Johnson, 2002; Cardillo, 2003). This effect can be either direct or indirect, mediated by the correlation of fecundity with geographical range size (Cooper et al., 2008). Our results support the indirect effect, as long as range size was the single best

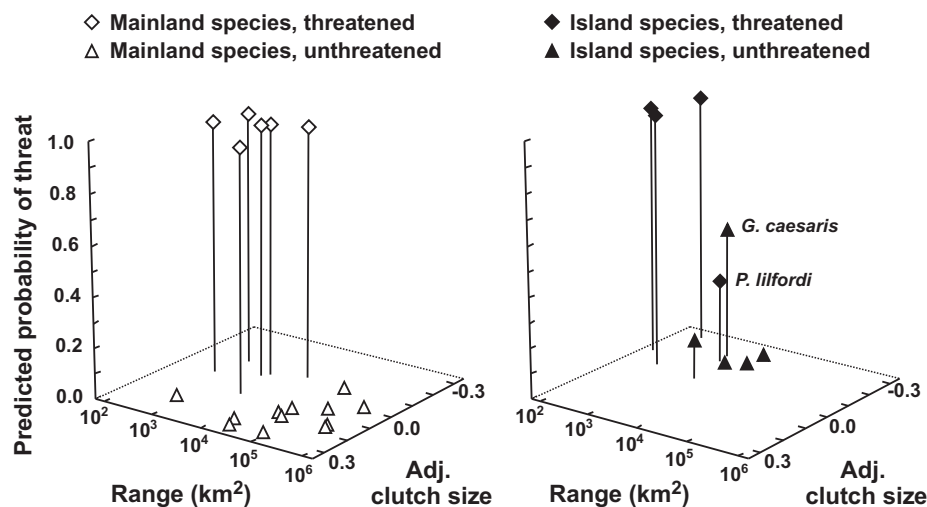


Fig. 3. Probability of threat for 27 species of mainland or inland lacertid lizards, as predicted by logistic regression model #4 in Table 3, plotted against the size of their distribution range and their SVL-adjusted clutch size (residuals of log-clutch size on log-SVL). Only two insular species were incorrectly predicted to be threatened (*Gallotia caesaris*: $P_{threat} = 0.516$) and non-threatened (*Podarcis lilfordi*: $P_{threat} = 0.333$), respectively.

predictor of extinction risk (and it explained most of the covariation between SVL-adjusted clutch size and conservation status). However, they also supported the direct effect, because SVL-adjusted clutch size was still lower for threatened mainland species after controlling for the effects of range size.

A second and more interesting result concerned insular species, which showed remarkably low clutch sizes independently of their degree of threat (Figs. 2 and 3). Thus, threatened mainland species had lower clutch sizes for their SVL than non-threatened ones, whereas all island species, independently of their conservation status, had low SVL-adjusted clutch sizes. Remarkably, the altitudinal range was smaller for threatened than for non-threatened species both on islands and on the mainland, with no interaction between these two predictors (Model 2 in Table 3). This supports the conclusion that the significant interaction found for clutch size is a biologically relevant finding rather than a statistical artifact. Because natality must balance mortality if populations are to persist over time, there is a direct putative causal link between low clutch size and high risk of extinction in mainland lacertids.

The low average clutch size of insular lizards compared with mainland species of their same body size was among the clearest results of both our conventional and phylogenetic analyses (Fig. 2). This result challenges one of the main conclusions of the comparative study of life-history covariation in mainland lacertids by Bauwens and Díaz-Uriarte (1997), namely that the negative allometry of offspring and adult size leads to a disproportionately large clutch size in the larger species. Several selective pressures may be responsible for the low fecundity of island lizards. One explanation could be the scarcity of food, specially arthropod prey (Janzen, 1973), which is consistent with the fact that among lacertids insularity is often associated with a change towards herbivory (Van Damme, 1999). In addition, the lack of natural predators may have promoted high population densities (Buckley and Jetz, 2007) leading to an advantage of large sized eggs and juveniles in intraspecific competition (Castilla and Bauwens, 1991), and large sized eggs seem to be favoured in low productivity environments (Abell, 1999; Iraeta et al., 2008). Given the trade-off between clutch and offspring size (Sinervo and Licht, 1991; Stearns, 1992; Bauwens and Díaz-Uriarte, 1997), selection for large eggs would also result in reduced clutch size.

Why some island species are critically endangered, whereas others reach densities that convert them into agricultural pests (e.g. *Gallotia galloti*, which can reach densities up to 3500 individuals/ha; de los Santos and de Nicolas, 2008), remains an open question. One possibility would be to invoke the larger size of the endangered species. It is widely acknowledged that the body size of island populations of terrestrial vertebrates is frequently different from that of mainland populations, sometimes following consistent patterns. One of such patterns is the 'island rule', or the tendency of small mammals to evolve larger sizes on islands than their mainland conspecifics, whereas the opposite would be true for large mammals (Foster, 1964; Lomolino, 1985). For squamate reptiles, the available evidence is inconclusive with respect to the generality of the island rule (Boback and Guyer, 2003; Meiri, 2007). According to our non-phylogenetic analysis, island lizards showed a tendency to reach larger sizes than their mainland relatives (Castilla and Bauwens, 1991; but see Van Damme, 1999), but the statistical significance of such trend disappeared in the phylogenetic ANOVA. Whatever its magnitude and causes, the large size of the bigger insular lacertids may pose significant threats to their preservation upon the arrival of introduced predators, given the limited evolutionary experience of insular taxa with biotic interactions (Buckley and Jetz, 2007). Moreover, the delayed maturity of the bigger species is expected to increase juvenile mortality, thereby decreasing recruitment rates (Bauwens and Díaz-Uriarte, 1997). However, it is also true that other behavioural and ecological

factors (e.g. aggressiveness, microhabitat preferences), perhaps correlated with phylogeny, must also be considered to explain the contrast between *Gallotia stehlini*, the giant lizard from the island of Gran Canaria (which can reach densities of up to 1000 individuals/ha; Pleguezuelos et al., 2002), and the critically endangered large-sized species from the Western islands of La Gomera (*G. bravoana*) and El Hierro (*G. simonyi*).

Because the proportion of threatened taxa did not differ between continental and insular species (despite the lower SVL-adjusted clutch size, range size and altitudinal range of the latter ones), insularity per se had a positive effect on resilience to extinction in all the predictive models in which it was included. This is consistent with the results of a previous study which has found that extinction risk is actually lower for insular than for continental bird species when holding for the effects of range size (Manne et al., 1999).

Concerning mainland lacertids, threatened species had lower relative fecundities than non-threatened ones, thus providing evidence of a direct relationship between life-history traits and conservation status (Cardillo, 2003; Hero et al., 2005). It should be noted that most of the endangered continental species were montane endemics with isolated populations in high-elevation areas. Because high elevations act like island habitats isolated by a heterogeneous mix of immigration filters (Lomolino and Davis, 1997; Monasterio et al., 2009), it might be thought that the life-history characteristics of these endangered species could be similar to those of truly insular lacertids. However, the environmental conditions and selective pressures that shape lizard life histories are quite different in mountains and in oceanic islands. Thus, many insular species lay in captivity two or even more clutches per year (Bannert, 1998; Castilla and Bauwens, 2000a,b), which might contribute to explain the lack of relationship between reduced fecundity and conservation status. However, of the two giant Canarian lizards for which there are enough data about reproduction in captivity, *Gallotia stehlini*, which is in the low concern category, lays only one clutch per year, whereas *G. simonyi*, which is critically endangered, may lay two clutches per year (Bannert, 1998).

On the other hand, the harsh climatic conditions of alpine habitats lead to very short lizard reproductive seasons, which allow only one clutch per year, limit annual growth, and delay sexual maturity. All these traits hamper the recruitment of juveniles, thus threatening the viability of populations and increasing their vulnerability to fragmentation and human alteration of the habitat (Arribas and Galán, 2005). Global warming might partly compensate for these effects, but a continuous rise in temperature could also decrease the amount of suitable alpine habitat available on the long term (Chamaille-Jammes et al., 2006; Monasterio et al., 2009). Also, climate change will likely result in changing community assemblages, potentially introducing new predators that alpine species may be ill-equipped to avoid.

Finally, we have to acknowledge that clutch size is only a component of overall fecundity, and that lacertids exhibit adaptive adjustments of life-history variables not for single characteristics but rather for suites of traits that promote increased reproductive output (Bauwens and Díaz-Uriarte, 1997). Hence, it is likely that other life-history traits may also predispose species to be at high risk. Our literature survey allowed us to gather data on mean egg mass and age at maturity for a smaller subset of the species included in Fig. 1 (data available as electronic Supplementary material). Remarkably, these traits were correlated with the ones reported here. For example, large eggs were produced by large sized, late maturing species with small SVL-adjusted clutch sizes, whereas age at maturity was positively correlated with SVL and egg mass and negatively correlated with distribution range size and relative fecundity.

Accordingly, conservation status could also be predicted, even after controlling for phylogenetic effects, by the interaction between insularity and SVL-adjusted age at maturity: on islands, but not on the mainland, threatened species of a given body size mature later than non-threatened ones (results not shown). A similar result was obtained for SVL-adjusted mean egg mass, at least in non-phylogenetic analyses: threatened species laid larger eggs than non-threatened ones on islands, but not on the mainland. This is a surprising outcome, given the well-known survival advantage of large juveniles (Stearns, 1992; Svensson and Sinervo, 2000), and it suggests that cause and effect relationships between life-history characteristics and risk of extinction are mediated by complex correlations among suites of traits. Nevertheless, a best subsets approach to model selection confirmed that the best predictor of extinction risk, after controlling for the effects of phylogeny, distribution range and insularity, was the interaction between SVL-adjusted clutch size and insularity (Model 4 in Table 3).

In summary, small SVL-adjusted clutch size (and associated life-history traits such as delayed maturity) was a good predictor of high extinction risk only in mainland species. On islands, it was integrated in an adaptive syndrome that, having evolved in low-productivity ecosystems with a scarcity of predators, may predispose to, but does not ensure, a high vulnerability to extinction. Our results emphasize the need to consider the interactions between the life-history characteristics of organisms and the environmental sources of threat, for a better understanding of the processes that cause variations in extinction risk.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.07.002.

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