Comparative chorology between *Podarcis bocagei* and *P. carbonellae* (Sauria: Lacertidae) in Portugal

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Abstract: The geographic distributions of the Bocage's wall lizard, *Podarcis bocagei* and the Carbonell's wall lizard, *P. carbonellae* in Portugal were determined through extensive field surveys. The river Douro constitutes the main geographical barrier where both lizard species show nearby a zone of contact. Predictive models of probability of occurrence were developed for both species in Portugal, based on the Logistic Multiple Regression (LMR) and the Overlap Analysis (OA). On a coarse scale, the best-fit model suggested that the distribution of *P. bocagei* in Portugal might be largely explained by macroenvironmental variables such as radiation, evapotranspiration or type of climate. The balance between the number of frost days per year and a coefficient of aridity (Kdr = 100 × temperature/precipitation) seems important to explain the range of *P. carbonellae.* However, the large overlap found between predictive areas strongly suggest that historical events (e.g. Pliocene speciation, Pleistocene glacial refugia) might have been preponderant, acting the macroenvironmental factors as ultimate determinants of the present-day distribution of both species. The distribution of *P. bocagei* is significantly congruent with that of *Chioglossa lusitanica*, partially with *Vipera seoanei* and with *Rana iberica* and *Lacerta schreiberi* northwards the river Douro. Conversely, the contractive distribution of *P. carbonellae* did not share any significant pattern of congruence with the latter taxa.
Key words: *Podarcis bocagei, Podarcis carbonellae*, Iberia, chorology, model, distribution.

Resumen: Corología comparativa entre *Podarcis bocagei* y *P. carbonellae* (Sauria: Lacertidae) en Portugal.- Las distribuciones geográficas de la lagartija de Bocage, *Podarcis bocagei* y de la lagartija de Carbonell, *P. carbonellae* en Portugal han sido determinadas mediante extensos muestreos en el campo. El río Douro constituye la barrera geográfica principal donde las dos especies de lagartijas presentan una zona de contacto. Los modelos preditivos de probabilidad de ocurrencia fueran desarrollados para ambas especies en Portugal, basados en la Regresión Logística Multivariada (LMR) y en el Análisis de Solapamiento (OA). En una larga escala, el modelo más ajustado sugiere que la distribución de *P. bocagei* en Portugal podría ser largamente explicada por las variables macroambientales como sean la radiación, evapotranspiración o el tipo climático. El balance entre el numero de días anuales con helada y el coeficiente de aridez (Kdr=100(temperatura÷precipitación) parece importante para explicar el rango de *P. carbonellae.* Entretanto, el gran solapamiento encontrado entre áreas predichas fuertemente sugiere que los eventos históricos (ej. especiación pliocénica, refugios glaciales pleistocénicos) podrían haber sido preponderantes, actuando los factores macroambientales como determinantes finales de la actual distribución de ambas especies. La distribución de *P. bocagei* es significativamente congruente con aquella de *Chioglossa lusitanica*, en parte con *Vipera seoanei* y al norte del río Douro, con *Rana iberica* y *Lacerta schreiberi*. Contrariamente, la contractiva distribución de *P. carbonellae* no comparte ninguno patrón de congruencia con los restantes taxa.
Palabras clave: *Podarcis bocagei, Podarcis carbonellae,* Iberia, corología, modelo, distribución.

INTRODUCTION

W Iberian herpetofauna

Within the Iberian herpetofauna, a group of Iberian-Atlantic species was put in relief as being endemic of W Iberia (cf. BAS & GASSER, 1994; ARRIBAS, 1996). Those species are: the golden-striped salamander, *Chioglossa lusitanica* Barbosa du Bocage 1864; the Bosca's newt, *Triturus boscai* (Lataste 1879); the Iberian brown frog *Rana iberica* Boulenger 1879; the Iberian rock lizard, *Archaeola-*

certa monticola (Boulenger 1905); the Schreiber's green-lizard, *Lacerta schreiberi* Bedriaga 1878; the Bocage's wall lizard, *Podarcis bocagei* (Seoane 1884); the Carbonell's wall lizard *Podarcis carbonellae* Pérez-Mellado 1981; and the Seoane's viper *Vipera seoanei* Lataste 1879 (SALVADOR, 1974; PÉREZ-MELLADO, 1981a, b; RIVA DE LA VIÑA, 1987; ESTEBAN & SANCHÍZ, 1991; BALADO *et al.*, 1995; ARRIBAS, 1996; PLEGUEZUELOS, 1997 and authors therein; SÁ-SOUSA, 2000a). Among those W Iberian species, *T. boscai* has the more extensive range at present (DÍAZ-PANIAGUA, 1997). Based on morphology, those taxa have also been considered so far as being monotypic or with few subspecies. Also, it has long been thought that those species, as well as the most modern vertebrate species in Europe, are recent and evolved during the Pleistocene (COX & MOORE, 1993). The cold/warm oscillations during the Pleistocene glaciations converted the W Iberia into an autonomous centre of (sub)speciation for the herpetofauna (BARBADILLO *et al.*, 1997, 1999). The W Iberia contained the largest European refugium of deciduous forest during the Würm (ZAGWIJN, 1992). Post-glacial warming up and the increment of humidity permitted the expansion of the Atlantic deciduous forest (8000-5000 BP), but since that time until nowadays the progressive aridity has been contracting the deciduous forest to NW Iberia (COSTA-TENORIO *et al.*, 1990). However, recent data strongly support the idea that many species are much more ancient and they speciated from the Miocene to the Pliocene (OOSTERBROEK & ARNTZEN, 1992; HEWITT, 1996, 1999; TABERLET *et al.*, 1998; BLONDEL & ARONSON, 1999). The Messinian Salinity Crisis (6.7-5.3 My BP) allowed the herpetofaunal interchange between Iberia and NW Africa through the Betic-Rifan landmass (HSÜ, 1983; BLONDEL & ARONSON, 1999). Several maxima of aridity had been attained in Iberia and W Europe until the Late Pliocene. In that time, the Iberian herpetofauna was mainly constituted by thermophile taxa, while other taxa had probably some cool, moist refugia somewhere in the coastal and mountain areas (BAILÓN, 1991, BARBADILLO *et al.*, 1997).

This study is focused on the comparative chorology of two ground-dwelling *Podarcis* lizards that live in W Iberia, also taking into account their distributional resemblance with other W Iberian herpetofauna. *P. bocagei* is a medium-sized (maximal SVL=65-70 mm) insectivorous lizard, whose males show green dorsal patterns, while females are brown with a pair of green stripes (PÉREZ-MELLADO, 1981, 1986, SÁ-SOUSA, 1995). This species occurs in W Asturias, Cantabria, Galicia and North of Portugal (GALÁN, 1986, 1997; SÁ-SOUSA, 1998). *P. carbonellae* is a greenish, small-sized (SVL=50-55 mm) lizard initially thought to be restricted to the W Sistema Central range (PÉREZ-MELLADO, 1981, 1986, 1997, 1998a). However, it has been found in other mountain systems as well as along Atlantic lowlands, particularly in Portugal (MAGRANER, 1986; SÁ-SOUSA, 1995, 1999, 2000a). *P. carbonellae* was recently recognised as a different species, differing from *P. bocagei* in several morphological features and constituting a divergent molecular lineage (HARRIS & SÁ-SOUSA, 2001; SÁ-SOUSA, submitted). However, *P. bocagei* and *P. carbonellae* are found in Portugal, where their parapatric distributions create a zone of contact without interbreeding established near the River Douro.

Chorological models

Predictive models of probability of occurrence were developed for both wall lizard species, based on the logistic multiple regression (LMR) and the overlap analysis (OA). The advantages and disadvantages of each two methods were discussed recently (BRITO *et al.*, 1999). Several macroenvironmental factors and others (e.g. glacial events, geographic barriers) were took into account, which could influence the chorology of *P. bocagei* and of *P. carbonellae* in W Iberia, particularly in Portugal.

Logistic Multiple Regression (LMR) has been shown to be a powerful tool, capable of analysing the effects of one or several independent variables, discrete or continuous, over a dichotomic (presence/absence) or polychotomic dependent variable (HOSMER & LEMESHOW, 1989). LMR model was obtained from a regression equation of the form $y=a+bx_1+cx_2+...+nx_i$, where a is the equation constant and $b, c, ...n$ are the coefficients of each i independent variable. Thus, the probability of occurrence of the species was calculated from $p= e^y \div (e^y+1)$, where e is the base of the Napieran logarithm (HOSMER & LEMESHOW, 1989; ANTÚNEZ & MENDOZA, 1992). LMR has been used recently to model some herpetofaunal distributions and habitat features (PAVIGNANO *et al.*, 1990; MANN *et al.*, 1991; ROMERO & REAL, 1996; BRITO *et al.*, 1996, 1999; SÁ-SOUSA, 2000b).

Nevertheless, an easier and faster method to obtain potential areas of species distribution is the Overlap Analysis (OA). This method simply combines variables with the presence of species, eliminating those with no explanatory power, and recombining the remainder varables. Maps of potential occurrence of species are obtained as well as information on the importance of each variable class for the species (BRITO *et al.*, 1999).

MATERIAL AND METHODS

Distributional resemblance

The presence/absence data available (Universal Transverse Mercator; UTM 50 x 50 km cells) for the eight W Iberian species considered came from PLEGUEZUELOS (1997 and authors therein). The distributional matrices also used information from other accurate atlases for Portugal and Galicia (e.g. CRESPO & OLIVEIRA 1989; BALADO *et al.*, 1995; MALKMUS, 1995; SÁ-SOUSA, 1998, 1999, 2000a), considering an entry is 1 if a species is present and 0 if it is absent. The Jaccard's coefficient (J) was applied on the binary matrices of presence/absence, assessing the distributional resemblances between species. Significant values of resemblance were assumed above the minimal J = 0.50 to-0.42, when N = 30 to 100, $p<0.05$, according to REAL *et al*. (1992a, b) and REAL (1999).

Chorological models

A set of macroenvironmental variables, assumed important for both wall lizards, was considered to determine suitable areas of occurrence. Eleven variables were extracted from macroenvironmental digital maps published by the Portuguese Ministry of Environment. Similar macroenvironmental charts were previously published as "Atlas do Ambiente" (see CNA, 1983). Both the digital maps and the charts represented mean annual variables (in classes). These macroenvironmental variables used were: RAD (radiation); INS (insolation i.e. number of hours of sun per year); TEMP (daily temperature of the air in degrees Celsius); PRE (total precipitation in mm per year); RAIN (number of days per year with rainfall); FRD (number of days with frost cover); FRM (number of months when frosty days may occur); HUM (humidity i.e. relative moisture of the air measured in percentage at 9h00 GMT); RUN (runoff i.e. amount of water yearly drained in the river basins); EVP (evapotranspiration i.e. the amount of water returned to the atmosphere); and CLIM (Atlantic component of climate expressed in relative percentage) - see for details SÁ-SOUSA (2000b).

All data (i.e. macroenvironmental variables and lizard records) were imported to a GIS (geographic information system), each as being a separate (raster) layer, keeping the spatial accuracy at least 1x1 km UTM. All chorological modelling was GIS assisted (i.e. Idrisi for Windows v.1.0 see EASTMAN, 1988).

The Logistic Multiple Regression (LMR) models were built with the Egret software (see EGRET, 1991). The building strategy followed a five-step procedure already used in SÁ-SOUSA (2000b) and recommended by HOSMER & LEMESHOW (1989) and BRITO *et al.* (1996, 1999). The Pearson chi-square (χ^2) test and a classification table were used to assess the fit of the LMR model (HOSMER & LEMESHOW, 1989; BRITO *et al.*, 1996, 1999). Classification tables were based on the dependent variable, with presence, absence and total cases of *P. bocagei* or *P. carbonellae*, using observed values and predicted values - the latter representing the estimated probability of occurrence, from the final LMR model (SÁ-SOUSA, 2000b). A cut-off point of 0.40 was used as a minimum probability for supporting presence.

Overlap Analysis (OA) models for predicted presence are obtained from the GIS-based overlap between each lizard presence layer and each macroenvironmental layers. Thus, classes were deleted when they did not overlap with the distributional layer of the species or they only included one presence. A final classification was performed by overlapping whether that potential area of occurrence with the layer of presences or the non-potential area with the layer of absences (see for details BRITO *et al.*, 1999).

Finally, the hypothesis of spatial autocorrelation in data was tested, using the simple normalised Mantel test on matrix comparison by a permutation procedure e.g. 5000 times (LEGENDRE & LEGENDRE, 1998). The matrix comparison was performed with NTSYS-PC 1.8 software (developed by F. James Rohlf).

RESULTS

Distributional resemblance

The Figure 1 shows the known distribution (UTM 10x10 km) for *P. bocagei* (49 cells) and for *P. carbonellae* (52 cells) in Portugal. The records from W Asturias, Galicia and W Sistema Central are also shown (data from PÉREZ-MELLADO, 1983; GALÁN, 1986; BALADO *et al.*, 1995).

In Table 1 is shown the distributional resemblances (Jaccard's coefficient) between *P. bocagei* - *P. carbonellae* and the ranges of 1) each remainder W Iberian species; 2) *R. iberica*, *L. schreiberi* and the sets of the superimposed distributions from any three (3sp) or five (5sp) other W Iberian species, respectively northwards or southwards the river Douro. Thus, the distribution of *P. bocagei* is rather congruent with that of *C. lusitanica* (J=0.60), partially with *V. seoanei*, while northwards the river Douro it resembles those of *L. schreiberi* (0.59), *R. iberica* (0.52) and where the ranges of any three W Iberian species are superimposed (0.69). Conversely, *P. carbonellae* did not share any significant pattern of resemblance with the other taxa. Even so its highest values of resemblance (J=0.22-0.28) are obtained against the ranges of *R. iberica*, *L. schreiberi* and any other three taxa (0.23) southwards the river Douro

Chorological models

The final LMR models for both *P. bocagei* and *P. carbonellae* were obtained when the input variables PRE, RAIN, FRM, HUM and INS were eliminated through the multivariate analysis. Among *P. carbonellae* models, the variables temperature and precipitation appeared as a ratio rewritten as the Dantin & Revenga's coefficient of aridity Kdr= 100(TEMPerature÷PREcipitation (see ALBUQUERQUE, 1954). The best-fit LMR model obtained for *P. bocagei* is y = 0.09851 CLIM + 0.008121 EVP - 0.2229 RAD + 20.09, with good correct classifications >75% (see Table 2). For *P. carbonellae* the equation model is y= 0.4064 - 0.6956(Kdr + 0.1057 CLIM + 3.844 Kdr - 10.95. However, the correct classifications are acceptable when they correspond to 65-75% of cases.

The Figure 2 shows that there is a good LMR fit between observed and predicted distributions for *P. bocagei* northwards the river Douro, while similar fit is only found for *P. carbonellae* southwards this river. However, both LMR models predicted for one species some areas of the range of the other species and vice-versa.

Table 1: Distributional resemblance (Jaccard's coefficient) found between the ranges of *P. bocagei* - *P. carbonellae* and each of remainder W Iberian species (in UTM 50x50 km). 5sp and 3sp correspond to the superimposed distributions of any five or three W Iberian species, respectively. Scientific names of species are abbreviated.

Tabla 1: Semejanza de las distribuciones (coeficiente de Jaccard) encontrada entre los rangos de *P. bocagei* - *P. carbonellae* y de cada una de las especies ibéricas occidentales (en UTM 50x50 Km). 5sp y 3sp corresponden respectivamente al soplamiento de las distribuciones de cualquiera cinco o tres especies ibéricas occidentales Los nombres científicos de las especies están abreviados.

	Range W Iberia				**northwards** the river Douro					**southwards** the river Douro				
Species	*C. lu.*	*T. bo*	*R. ib*	*L. sc*	*A. mo*	*V. se*	*R. ib*	*L. sc*	*5sp*	*3sp*	*R. ib*	*L. sc*	*5sp*	*3sp*
P. bocagei	0.60	0.30	0.38	0.39	0.39	0.47	0.52	0.59	0.47	0.69	0.05	0.03	0.00	0.04
P. carbonellae	0.08	0.13	0.12	0.13	0.05	0.00	0.00	0.00	0.00	0.00	0.22	0.28	0.06	0.23

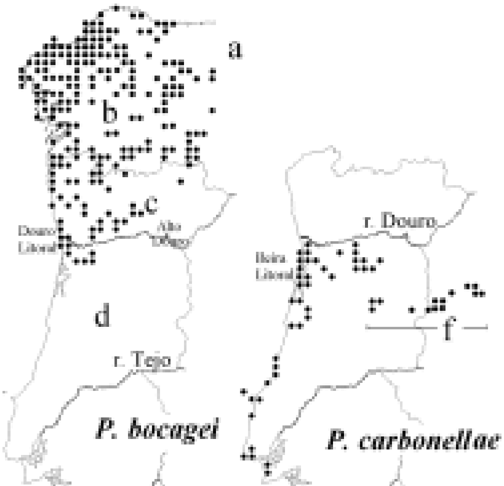

Figure 1.- Distribution for *P. bocagei* (left map) and *P. carbonellae* (right map) known in W Iberia and Portugal (after PÉREZ-MELLADO, 1983; GALÁN, 1986; SÁ-SOUSA, 1998, 1999, 2000a). Regions referred in the text: W Asturias (a), Galicia (b); Northern (c), Central (d) and Southern Portugal (e); W Sistema Central mountain range (f) and Coto Doñana (g).

Figura 1.- Distribución de *P. bocagei* (mapa izquierdo) y de *P. carbonellae* (mapa derecho) conocida en Iberia Occidental y Portugal (según PÉREZ-MELLADO, 1983; GALÁN, 1986; SÁ-SOUSA, 1998, 1999, 2000a). Regiones referidas en el texto: Asturias occidental (a), Galicia (b); Portugal al norte (c), al centro (d) y al sur (e); Sistema Central occidental (f) y Coto Doñana (g).

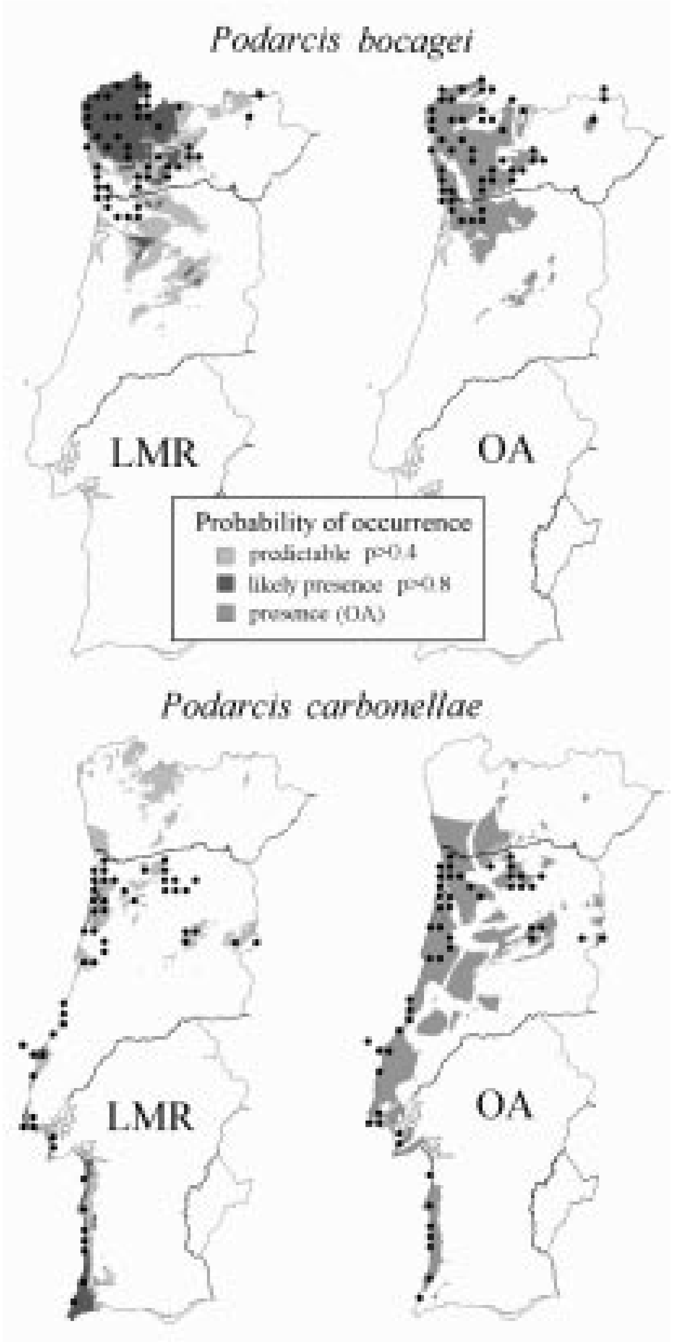

Figure 2.- Illustration of the predictive distributions of W Iberian *Podarcis* lizards (grey shades) obtained to Portugal from the Logistic Multiple Regression (LMR) and Overlap Analysis (OA).

Figura 2.- Representación de las distribuciones predictivas po las lagartijas *Podarcis* del Oeste Ibérico (gris) obtenidas para Portugal a partir de la Regresión Logística Multivariada (LMR) y del Análisis de Soplamiento (OA).

Table 2: Results of correct classifications obtained with the final models of the Logistic Multiple Regression (LMR) and Overlap Analysis (OA).
Tabla 2: Resultados de las clasificaciones correctas obtenidas en los modelos finales de Regresión Logística Multivariada (LMR) y del Análisis de Soplamiento (OA).

Species	Model	Presence	Absence	Total	χ^2-test	df
P. bocagei	LMR class.	69%	76%	73%	p<0.05	105
	LMR valid.	83%	89%	87%	p<0.01	26
	OA	79%	77%	78%		
P. carbonellae	LMR class.	67%	72%	70%	p<0.025	134
	LMR valid.	77%	59%	66%	n.s.	29
	OA	81%	62%	68%		

All initial macroenvironmental variables were kept during the overlap analysis (OA), though some classes were removed. The final OA models predicted patterns for both species that are roughly similar to those obtained with the LMR models, but (Figure 2). Once more the correct classifications obtained for *P. bocagei* are greater than those found for *P. carbonellae*, particularly with the absence cases. The spatial autocorrelation appears significant for some macroenvironmental variables used, which may reflect a strong interdependence between them (Table 3).

Table 3: Simple normalised Mantel test of matrix correlation between the spatial matrix (i.e. geographic distances between sites) and each macroenvironmental distance matrix, after 5000 permutations (*p<0.05, **p<0.0005, one-tailed).
Tabla 3: Teste de Mantel normalizado simples de la matriz de correlación entre la matriz espacial (i.e. distancias geográficas entre sitios) y cada una matriz de distancias macroambiental, después de 5000 permutaciones (* p<0.05, **p<0.0005, unilateral).

Macroenvironmental distance matrices	Spatial matrix *P. bocagei*	Spatial matrix *P. carbonellae*
N	42	45
Radiation (RAD)	0.464**	
Evapotranspiration (EVP)	0.427**	
Frost (FRD)		0.185*
Climate (CLIM)	0.166*	0.676**
Aridity (Kdr)		0.756**

DISCUSSION

The two main reasons that explain why so many records of *P. bocagei* and of *P. carbonellae* have been added are: (1) most of the Portuguese data were previously referred together as being the complex of *P. bocagei* - *P. hispanica* (cf. CRESPO & OLIVEIRA, 1989; MALKMUS, 1995); and (2) there had been inadequate sampling of *Podarcis* in Portugal.

The correct classification for the LMR models selected is still reliable for both species, but it is lower than that (>80%) found with *P. hispanica* (Sá-Sousa 2000a). Actually, the ranges of *P. bocagei* and *P. carbonellae* replace each other around the river Douro, biasing their predictive models by take into account many observed absences where the macroenvironmental conditions are suitable to predict presences (Table 2, Figure 2). The OA correct classification for *P. bocagei* is 10% higher than for *P. carbonellae*. That may be explained by the more disruptive distribution of the latter species (Figure 1 and 2), while the macroenvironmental variables were taken in broad scale. Also, OA allows less predictability (see BRITO *et al.*, 1999).

The relative importance of some macroenvironmental factors may be generalised from the models. Although, both species live where Atlantic conditions prevail, *P*. *bocagei* predominates in areas where the Atlantic influenced climate (CLIM) >70%, the evapotranspiration > 650 mm/year and the radiation <145 kcal. cm^2, reflecting indirectly cloudy/moist areas where often rains. *P. carbonellae* seems to be constrained to Atlantic or Sub-Atlantic areas that often are surrounded by major Mediterranean areas (PÉREZ-MELLADO, 1981, 1983, 1986, 1997, 1998a). That might be expressed in the LMR model equation through the balance between the possibility of frost (FRD) and the coefficient of aridity (Kdr).

The macroenvironmental variables used for models were included because of their likely biological significance, whereas they only reflect the annual integration of mean values. Thus, the final set of model predictions was largely derived on statistical grounds. The high spatial autocorrelation found with some macroenvironmental variables (Table 3) imply that subsequent relationship between lizard distribution and specific macroenvironmental variables cannot be assumed to imply causal effect. Probably, that spatial autocorrelation is an indirect result from the contractive distribution of lizards, particularly for *P. carbonellae.* If some macroenvironmental factors may play an important role, they are not the only factors that determine the distribution of these lizards. For instance, the habitat selection seems to slightly differ between both species. Although *P. bocagei* as well as *P. carbonellae* are ground-dwelling lizards, the first species seems more eclectic in its habitat use (SÁ-SOUSA, 2001). Nevertheless, both species occupy since open areas of deciduous forests of Olm Oak *Quercus pyrenaica* and its successional scrubland, meadows, rural plots, until the scrubby dunes (GALÁN, 1986; MAGRANER, 1986; PÉREZ-MELLADO, 1997, 1998a; SÁ-SOUSA, 2001). Actually, it seems that historical events might be preponderant, acting the macroenvironmental factors as ultimate determinants of distribution for both species. Otherwise, habitat features may be unsuitable in areas that are climatically ideal for those species.

Historical factors could have played an important role in determining present-day distributions (ANTÚNEZ & MENDOZA, 1992; GASTON, 1996), but this remains rather speculative for both species. Two related explanatory hypotheses, which differ in the space-time scale, are discussed here: (1) biogeographical traits reported back to Late Miocene-Pliocene; and 2) post-glacial range expansion from Pleistocene refugia, but followed by further contraction of range (at least in *P. carbonellae*) in the Holocene warming-up.

P. carbonellae was considered a subspecies of *P. bocagei* for a while and thus it might be thought that they are related species. Conversely, the high degree of molecular differentiation (9-9.6% between the COl sequences and 13.5-15.5% between the cytochrome *b* sequences) found between both species suggests that their processes of speciation are independent and they should be occurred at least in the Pliocene (HARRIS & SÁ-SOUSA, 2001). In that time several maxima of aridity had been attained in Iberia and the Iberian–Atlantic herpetofauna had probably some cool, moist refugia somewhere in the coastal and mountain areas (BAILÓN, 1991, BARBADILLO *et al*., 1997). Furthermore, *P. bocagei* and *P. carbonellae* have a narrow zone of contact where individuals with an intermediate appearance have not been found (SÁ-SOUSA, 1998, 2000a; personal observations). That is in accordance with the status of two separated species (MAYR & ASHLOCK, 1991; SÁ-SOUSA *et al*., 2000; HARRIS & SÁ-SOUSA, 2001).

Otherwise, the genetic diversity is very low 0-0.06% within *P. bocagei* and 0.004-0.09% within *P. carbonellae* (HARRIS & SÁ-SOUSA, 2001). This pattern suggests a bottleneck effect i.e. a rapid post-glacial colonisation northwards departing from southern small refugia placed elsewhere. However, some authors have been suggested that the ancestral speciation of *P. bocagei* occurred in NW Iberia, where it is widespread nowadays (SALVADOR, 1974; GALÁN, 1986; BALADO *et al*., 1995; PÉREZ-MELLADO, 1998a; BARBADILLO *et al*., 1999). But *P. bocagei* only colonised the islands off northern Galicia. This pattern suggests that the rupicolous *P. hispanica* (type 1) might arrive to Galicia before *P. bocagei*, though colonising no more than the mainland and all islands off Southern Galicia, because of climatic constraints (see MATEO, 1990; BALADO *et al*., 1995; SÁ-SOUSA, 2000a). The environmental conditions in Galicia (and many parts of north of Portugal) were hardly suitable for *P. bocagei*, during the Würmian glaciation, and so its expansion there might occur subsequently to the warm Atlantic phase (COSTA-TENORIO *et al*., 1990; ZAGWIJN, 1992; BALADO *et al*., 1995). In contrast, the persistence of glaciers on the NW Iberian mountains and a mighty river Douro might have constituted a ring barrier that constrained the expansion of *P. bocagei* (see BAS & GASSER, 1994; BALADO *et al*., 1995; DIAS *et al*., 1997; VIEIRA, 1998). As consequence, the presumed glacial refugium for *P. bocagei* was probably settled in NW Portugal, northwards the river Douro: near the coast or within Alto Douro, an actual Mediterranean enclave. If not, the absence of *P. bocagei* is hardly justified by environmental reasons in many Atlantic areas found southwards the river Douro, where *P. carbonellae* lives. For example, the central mountain regions (e.g. Sistema Central) constitute good candidates for the localisation of the past glacial refugia of *C. lusitanica* and *L. schreiberi* (ALEXANDRINO *et al*., 1997; PAULO *et al*., 1999). There, the species might have moved between the mountains (interglacial) and the river valleys (glacial), throughout at least the Pleistocene (PAULO *et al*., 1999). Other potential refugia were the coastal areas. In fact *P. carbonellae* colonised all the few islands (e.g. Berlengas, Baleal, Pessegueiro) off the W Portuguese coast, while the more abundant *P. hispanica* (type 2) did not (SÁ-SOUSA, 2000a, b; SÁ-SOUSA *et al*., 2000). Nowadays, *P. carbonellae* is relatively abundant in the province of Beira Litoral, where this lizard should be recent, because that lowland region were submerged (up to 50m a.s.l.) by the Atlantic ocean during the Flandrian transgression (5000 y BP). Also, *P. carbonellae* lives in the lower limits of climatic tolerance in many coastal areas southwards the river Tejo (=Tagus), where it strictly occurs in dune areas faced to the moist NW winds that came from the sea. Thus, it seems clear that *P. carbonellae* had a large range southwards the river Douro, where it evolved and probably had some glacial refugia. Moreover, some areas (e.g. Guadalupe Mts., Toledo Mts., Sierra Morena) where *L. schreiberi* occurs (RIVA DE VIÑA, 1987; BRITO *et al*., 1996, 1998) seem to constitute potential areas to the occurrence of *P. carbonellae*.

Nowadays, the river Douro separates the ranges of both lizard species. The upper valley of Douro (=Alto Douro, Figure 1) is a climatic barrier since it is a known Mediterranean enclave (RIBEIRO, 1987). From there, *P. bocagei* occurs in the mountains placed northwards e.g. Serra do Marão, Serra do Alvão, Serra da Nogueira, while *P. carbonellae* is in the mountains placed southwards e.g. Serra do Arestal, Serra de Montemuro, Serra de Leomil, Serra da Lapa (SÁ-SOUSA, 1998, 1999, 2000a). But *P. bocagei* has been also found southwards the river Douro e.g. dunes of Aguda-Espinho; county of Feira, Serra da Freita, where some cases of sintopy with *P. carbonellae* have been recorded (Figure 1; SÁ-SOUSA, 1998, 2000a, personal observations). That probably means a recent colonisation of *P. bocagei* provided by the several road bridges that have been built across the river Douro. If there is a competitive displacement between both species, *P. bocagei* might take some advantage.

However, the competitive colonisation of the European stock of *P. muralis* into Asturias and into the eastern part of Sistema Central (see CAPULA, 1997) probably constrained the expansion eastwards of *P. bocagei* and *P. carbonellae* respectively, subsequently to the warming-up post-Pleistocene (GALÁN, 1986; PÉREZ-MELLADO, 1986, 1998b). Similar situations were remarked with other pairs of species e.g. *Lacerta schreiberi* vs. *L.* (*viridis*) *bilineata*, *Vipera seoanei* vs. *V. aspis*, *V. latastei* (PLEGUEZUELOS, 1997 and authors therein).

Future research should aim at improving the chorological models by incorporating descriptors of habitat quality and other relevant variables. The results could also be improved either by changing the scale to more precise one or by using different modelling approaches e.g. trend surface models and Bayesian integrated statistical inference (PEREIRA & ITAMI, 1991; LEGENDRE & LEGENDRE, 1998). Nevertheless, both LMR and OA models can be used as useful clues for further detailed surveys on the distribution gaps of those lizards. Another obvious improvement is to extent the modelling to the whole Iberian range of both species, though that needs a good calibration of macroenvironmental descriptors, such as they are not easily compared yet, through the available data from Portugal and Spain.

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