A PREDICTIVE DISTRIBUTION MODEL FOR THE IBERIAN WALL LIZARD (*PODARCIS HISPANICUS*) IN PORTUGAL

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The geographic distributions of two forms of the Iberian wall lizard (*Podarcis hispanicus*) in Portugal were determined through extensive field surveys. Predictive models of probability of occurrence were developed for both forms of *P. hispanicus*, based on multivariate logistic regression of environmental variables. On a coarse scale, the best-fit models suggested that the distribution of the north-western form of *P. hispanicus* can be largely explained by environmental variables such as altitude, mean annual temperature and number of frost days per year. The distribution of the south-western form of *P. hispanicus* is also explained by altitude and temperature, but the type of climate also appears important. Predicted probabilities of occurrence broadly match the known distributions range of the two forms. Where predicted distributions are not confirmed by field surveys, historical and/or interspecific factors may be more important than environmental variables in influencing the distribution of the lizard.

Key words: *Podarcis*, wall lizard, distribution, GIS

INTRODUCTION

Podarcis hispanicus Steindachner 1870 is a small-bodied lizard (adult snout-vent length 65-70 mm), that is found in south-west France (Languedoc-Rousillon and Cévennes; the Iberian Peninsula (except the northernmost border area) and north-west Africa (see Fretey, 1986; Galán, 1986; Guillaume, 1987, 1997). It exhibits pronounced sexual dimorphism (the adult males being larger than the females and having a more intense pattern) and a strong polymorphism between populations (Barbadillo, 1987; Pérez-Mellado & Galindo, 1986; Salvador, 1986). *P. hispanicus* is mainly saxicolous and inhabits rocky shores, stone piles, walls and other stone constructions, with variable vegetation cover (Pérez-Mellado, 1983a, 1997a; Salvador, 1986). Where *P. hispanicus* is the only representative of the genus *Podarcis* (i.e. the centre, the south, and parts of the eastern coast of the Iberian Peninsula), it is ubiquitous and an opportunist, occupying all the available natural or semi-natural habitats (Guillaume, 1997). It feeds mostly on Arachnidae, Diptera, Homoptera, Hymenoptera, Coleoptera, Formicidae and insect larvae (Pérez-Mellado, 1983b; Salvador, 1986; Barbadillo, 1987).

Although *P. hispanicus* is potentially widespread in Portugal, distribution records are not abundant, because the majority of the data refer to the *P. bocagei/P. hispanicus* complex (e.g. see distribution maps from Crespo & Oliveira, 1989; Malkmus, 1995). According to Crespo & Oliveira (1989) their "complex" classification was a prudent way of dealing with an incomplete data set, as the classification of *Podarcis* in Portugal is unclear. Moreover, some apparent gaps in the *P.*

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hispanicus distribution in Iberia (e.g. "Submeseta Sul" plateau, Andalusia and South of Portugal) have been identified as a result of inadequate sampling (Pérez-Mellado, 1997a). In fact, *P. bocagei* and *P. hispanicus* are morphologically and ecologically distinct species that live sympatrically in Galicia and northern and central Portugal (Arnold & Burton, 1978; Pérez-Mellado, 1981; Galán, 1986; Barbadillo, 1987). Despite the taxonomic controversy concerning *P. hispanicus*, I have studied the morphology of two distinct allopatric forms of this wall lizard in Portugal (Sá-Sousa, 1995 and unpubl. data). Firstly, there exists a north-western Iberian form (*P. hispanicus* 1) found in Galicia, the "Submeseta Norte" plateau, northern and central Portugal, and the "Sistema Central" range (i.e. the form *P. h. "lusitanica"* described by Guillaume, 1987). This form has the following characteristics: head and body very depressed; mainly dark, reticulated, marbled and/or striped dorsal patterns; whitish or pearly belly (for details see Pérez-Mellado, 1981; Galán, 1986; Pérez-Mellado & Galindo, 1986; Guillaume, 1987; Galán & Fernández, 1993; Balado, Bas-López & Galán, 1995; Sá-Sousa, 1995). Secondly, there is a south-western Iberian form (*P. hispanicus* 2) first described from the Algarve as *Lacerta muralis* var. (=*Podarcis hispanicus*) *vaucheri* by Boulenger (1905). This form has the following characteristics: head and body moderately robust; mainly light brown and/or pale greenish dorsal patterns, yellow or orange belly (see Klemmer, 1959; the description of the "Andalucia/Portugal meridional" sample in Pérez-Mellado & Galindo, 1986; Salvador, 1986; Malkmus, 1995; Guillaume, 1987; González de la Vega, 1989; Sá-Sousa, 1995). Thus *P. hispanicus* 2 is known at least from the Algarve and Andalusia and for some of these authors it may also be synonymized with the present Maghrebian wall lizard subspecies *P. hispanicus vaucheri*. Moreover, Busack (1986) found a low ge-

netic distance (D_{Nei}=0.07) between Andalusian and Moroccan populations of *P. hispanicus*.

The factors that determine the distributional range of a species are often diverse and subject to complex interactions. According to Wiens (1989), Antúnez & Mendoza (1992) and Cox & Moore (1993), they can mainly be classified as: (1) presence of barriers (e.g. large rivers, mountain ranges, ice caps, sea extensions, etc.); (2) absence of suitable habitat (i.e. scarcity of certain resources or climatic constraints); (3) non-availability of sufficiently large areas to support viable populations; (4) interactions with other species (e.g. interspecific competition, predation, parasitism, mutualism, influence of man); (5) history (if any of the factors cited above have played a role in the past, then their effect will influence the present distribution); and (6) chance events that may have influenced the present distribution.

Climatically, Portugal shows an important latitudinal intergradation between two greater climate domains, the Atlantic (ΣA) and the Mediterranean (ΣM), both interacting with the altitudinal gradient created by relief (Albuquerque, 1954; Ribeiro, 1987). How environmental conditions might influence the *P. hispanicus* distribution was the major aim of this work. This was pursued by (1) updating the distribution in Portugal with recent field surveys; and (2) deriving predictive models for the general distribution, using logistic regression in order to evaluate the probability of occurrence of the two forms of *P. hispanicus* in Portugal.

Given the binary nature of the wall lizard distribution data and the qualitative or non-multivariate normal nature of some available environmental data, logistic regression was considered as more appropriate for modelling the distribution (Press & Wilson, 1978; Hosmer & Lemeshow, 1989; Pereira & Itami, 1991; Austin, Thomas, Houston & Thompson, 1996). Logistic regression is used as a tool for analysing the effects of one or several independent variables, which may be either discrete or continuous, on one dependent binary variable (e.g. presence/absence). It has been used recently for modelling lizard distributions (Brito, Brito e Abreu, Paulo, Rosa & Crespo, 1996); and to study amphibian habitat features (Pavignano, Giacoma & Castellano, 1990; Mann, Dorn & Brandl, 1991; Romero & Real, 1996) as for other vertebrate species (Walker, 1990; Pereira & Itami, 1991; Gates, Gibbons, Lack & Fuller, 1994; Austin *et al.* 1996). The model for logistic regression has the form: $p(y) = e^y/(1 + e^y)$ where e is the base of the Naperian logarithm, and $p(y)$ is the probability of occurrence of the species. The value y is obtained from a regression equation of the form $y = a + b\,x_1 + c\,x_2 + ... + n\,x_n$, where a is the equation constant and $b, c, ...$ are the 1 to n coefficients of the x independent variables (Hosmer & Lemeshow, 1989). A multivariate logistic regression model, based on environmental variables, was used to predict the probability of occurrence of each *P. hispanicus* form in Portugal.

Spatial autocorrelation between physical environmental variables is problematical for statistical testing as autocorrelated data violate the assumption of independence of most standard statistical procedures. Moreover, physical environmental variables are not distributed uniformly or randomly (Legendre, 1993). There are two main sources of spatial autocorrelation: (1) geography, whereby adjacent values tend to be strongly related (Augustin, Mugglestone & Buckland, 1996); and (2) "spatial structure", wherby the surface pattern or the distribution of physical environmental variables tends to change gradually (Legendre, 1990; Dutilleul, 1993).

MATERIAL AND METHODS

DISTRIBUTION RECORDS

The sampling strategy was mainly based on field-work surveys of new *P. hispanicus* 1 and *P. hispanicus* 2 locations in Portugal. Some records were initially obtained by studying preserved specimens in the Museu Bocage (the Natural History Museum of Lisbon). Other data were cited in literature such as Malkmus (1981, 1984*a,b*, 1985, 1987, 1990*a,b*, 1991, 1992, 1993*a,b*, 1995, 1997*a*), Meek (1983), Pérez-Mellado (1984), Galán (1986), Pérez-Mellado & Galindo (1986), and Ferrand de Almeida (1991). The majority of the new distribution data were obtained during four years of fieldwork, between 1993 and 1997. Two records of *P. hispanicus* 2 were recently obtained from Schwarzer (1998).

To determine potential areas of occurrence, a set of environmental characteristics, assumed to be important for wall lizards, was considered. Nine variables were extracted from 1:1 000 000 environmental digital maps published by the Portuguese Ministry of the Environment. Similar environmental charts were previously published as "Atlas do Ambiente" (see CNA, 1983). Both the digital maps and the charts represented annual environmental variables (in classes), illustrated as contours. The environmental variables used were: number of hours of sun per year (*insolation*); annual mean daily temperature of the air in degrees Celsius (*temperature*); mean total precipitation in mm per year (*precipitation*); number of days per year with rainfall (*rain*); relative number of days per year with frost cover (*frost* I); annual period (in months) when frosts may occur (*frost* II); mean annual relative moisture of the air, measured daily at 0900 GMT (*humidity*); amount of water yearly drained in to the river basins (*run-off*); and the amount of water returned to the atmosphere annually (*evapotranspiration*). The type of climate (*climate*) map was firstly digitized from the "Carta Ecológica" chart, and qualitative data were converted to percentage values of Atlantic influence within each type of climate (SA), following Albuquerque's (1954) tables - see correspondence values in the two last columns of Appendix 1. Both location coordinates and *altitude* (above sea level) were recorded during surveys, by consulting 1:250 000 charts. All the digital maps were

imported to a Geographical Information System (GIS; Idrisi for Windows 1.0, following Eastman, 1988). With the GIS, digital maps were equalized and geo-referenced to each other as well as to a digital UTM (Universal Transverse of Mercator) grid. *P. hispanicus* distribution points (UTM 1 x 1 km grid accuracy) were imported by GIS as a separate (raster) layer. The environmental database was extracted by GIS, producing cross-tabulation between the point distribution layer and each of the environmental layers. The *altitude* data column was assigned to this database at the end.

CONSTRUCTING THE PREDICTIVE MODELS

In order to reduce spatial autocorrelation, the sampling involved the selection at random of records (only one record for each UTM 10 x 10 km cell) and the acquisition of one validation sub-sample to be run apart. Thus each *P. hispanicus* distribution set, available as presence (P) / absence (A) data (dependent variable) consisted of two random sub-samples. One main sub-sample (>80%), with 109 present and 112 absent locations for *P. hispanicus* 1; and 112 present and 151 absent locations for *P. hispanicus* 2, was used to build and assess the fit of the models. One validation sub-sample (>20%), with 30 present and 28 absent locations for *P. hispanicus* 1, and 28 present and 43 absent locations for *P. hispanicus* 2, was used to test the prediction accuracy of the final models.

To determine the final regression models, the programme EGRET (1991) was used to undertake a five step procedure of building and evaluating multivariate logistic regressions, as suggested by Hosmer & Lemeshow (1989) and Brito *et al.* (1996). First, univariate logistic regression analysis (maximum likelihood ratio test G) was used to detect relevant environmental variables that showed a significative association with the binary dependent variable, i.e. the Wald test set at $P<0.25$ and the Odds ratio test with the 95% confidence interval not including 1.00 or not being overestimated (Hosmer & Lemeshow, 1989). The Odds ratio is a measure of association which approximates how likely (or unlikely) it is for the outcome to be present among those with $x=1$, rather than among those with $x=0$ (Hosmer & Lemeshow, 1989). Second, all variables selected by univariate analysis were included in a preliminary multivariate model carried out using a backward elimination procedure: each variable was removed stepwise from the model, in descending order of its previous univariate G-test value (Brito *et al.*, 1996). The only environmental variables that were considered relevant were those that abruptly decreased the G value when they were removed from the multivariate model. Those variables that showed a low level of association between the environmental variable and the presence/absence of the species were also eliminated. Third, up to four variables obtained in this way were checked for linearity. I assumed non-linearity if any transformed variable (i.e. x^2, $\log(x)$, $x\ln(x)$) provided a better fit according to the G or Wald tests than the initial variable (x), by univariate analysis. If so, the transformed variable was included in the model, instead of the initial variable, and used in subsequent analyses (see Hosmer & Lemeshow, 1989; Gates *et al.*, 1994, for details). Fourth, any confounding effect was checked for by adding all the initial variables, one after the other, to the last multivariate model in order to find any significant simultaneous increase in the G value. Fifth, significant interactions between variables were assessed again on the basis of significant increments in the G value.

FITTING THE PREDICTIVE MODELS

To assess the fit of the model, the Pearson chi-square and classification tables were used (Hosmer & Lemeshow, 1989; Brito *et al.*, 1996). The Pearson chi-square was calculated as follows: O_i is the observed value and P_i is the predicted value estimated from the model of logistic regression, where $P_i(y) = e^y / (1+ e^y)$.

Classification tables were based on the dependent variable, with presence, absence and total cases of the *P. hispanicus* 1 or *P. hispanicus* 2 forms, using observed values (P, A, T) and predicted values (P, A, T) - the latter representing the estimated probability of occurrence, from the multivariate models. A cut-off point of 0.50 was used as a minimum probability for supporting presence.

TESTING FOR SPATIAL AUTOCORRELATION

According to Legendre (1990), there are various ways of testing the hypothesis of spatial autocorrelation in data. The method used was the simple normalized Mantel (1967) test of matrix correspondence, incorporating the "spatial structure" into modelling using a matrix approach (Legendre, 1990, 1993). First, the spatial structure is assembled into a matrix, called SPACE, comprising geographical distances between the sampling locations (i.e. SPACE contains their Euclidean distances from UTM 1 x 1 km coordinates). Second, each environmental variable matrix is computed comparing locations with the Bray & Curtis (1957) percentage difference as resemblance coefficient. Third, a matrix correlation (simple Mantel test) between SPACE and each environmental matrix is tested by a permutation procedure (e.g. 200 repeated random permutations of the rows and columns), measuring the extent to which the variations in the distances of SPACE correspond to the variations in each environmental matrix. The null hypothesis to be tested is that those variations in the distances do not have linear correspondence with the pair(s) of matrices (SPACE and environmental variable). The matrix comparison was performed with NTSYS-PC 1.8 program (developed by F. James Rohlf).

DISTRIBUTION MAPS

P. hispanicus 1 and *P. hispanicus* 2 distribution maps were updated on a UTM 10 x 10 km based grid, distinguishing the new data (filled circles) obtained

during this work from the data previously known (open circles). The *P. hispanicus* 1 or *P. hispanicus* 2 probability of occurrence maps were generated with contours, using the GIS map algebra to run the model equations. The updated and the predicted distributions were overlain as a composite map. Two classes of probability of occurrence above the cut-off point of 0.5 were illustrated: predictable *P*=[0.5-0.8] and likely presence *P*>0.8.

RESULTS AND DISCUSSION

KNOWN DISTRIBUTION

Figs. 1-2 illustrate the distribution of *P. hispanicus* (UTM 10 x 10 km grid) in Portugal, including the new data: a total of 173 cells for *P. hispanicus* 1, of which 133 cells (77%) are new records, and a total of 185 cells for *P. hispanicus* 2, of which 164 cells (88%) are new records. Some records from neighbouring regions of Spain (i.e. Galicia, Castilla-Léon Extremadura and Andalusia) are also shown (data from Pérez-Mellado, 1983c; Galán, 1986; Pérez-Quintero, 1990; Palomo,

1993; Balado *et al.*, 1995). The two main reasons that explain why so many records have been added are: (1) that as previously stated, most of the Portuguese data referred only to the *P. bocagei/P. hispanicus* complex (cf. Crespo & Oliveira, 1989; Malkmus, 1995); and (2) that there had been inadequate sampling in Southern Iberia e.g. 'Submeseta Sul', part of Andalusia and southern Portugal were previously little known (Pérez-Mellado, 1997a).

PREDICTED DISTRIBUTION

To obtain final models for both *P. hispanicus* 1 and *P. hispanicus* 2, the input variables *insolation*, *humidity*, *evapotranspiration*, *rain* and *frost* II were initially eliminated in the univariate analyses. In the backward multivariate analysis, the variable *run-off* was excluded, while *frost* I and *climate* were only eliminated in the *P. hispanicus* 1 models. Among many models produced and tested, only the first best-fit model was chosen for each of *P. hispanicus* 1 and *P. hispanicus*. 2 (see Table 1). Both models explained significantly
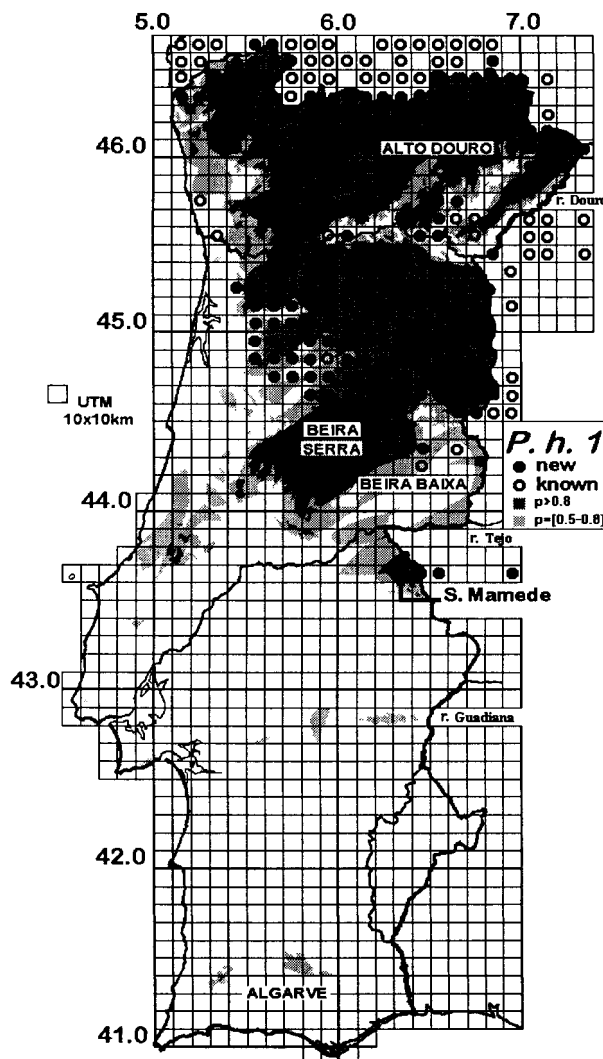

FIG. 1. Both updated (black circles) and predicted (grey contours) distributions of *P. hispanicus* 1(i.e. NW Iberian form). Probability of occurrence was based on the first best-fit model (Table 1). Grid: UTM 10 x 10 km.
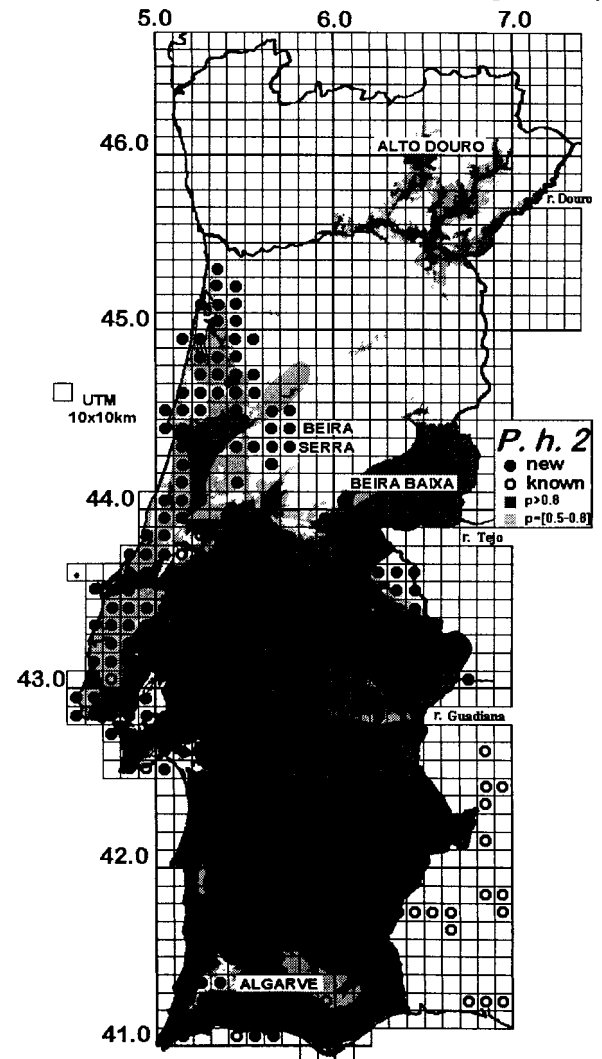
FIG. 2. Both updated (black circles) and predicted (grey contours) distributions of *P. hispanicus* 2 (i.e. SW Iberian form). Probability of occurrence was based on the first best-fit model (Table 1). Grid: UTM 10 x 10 km.
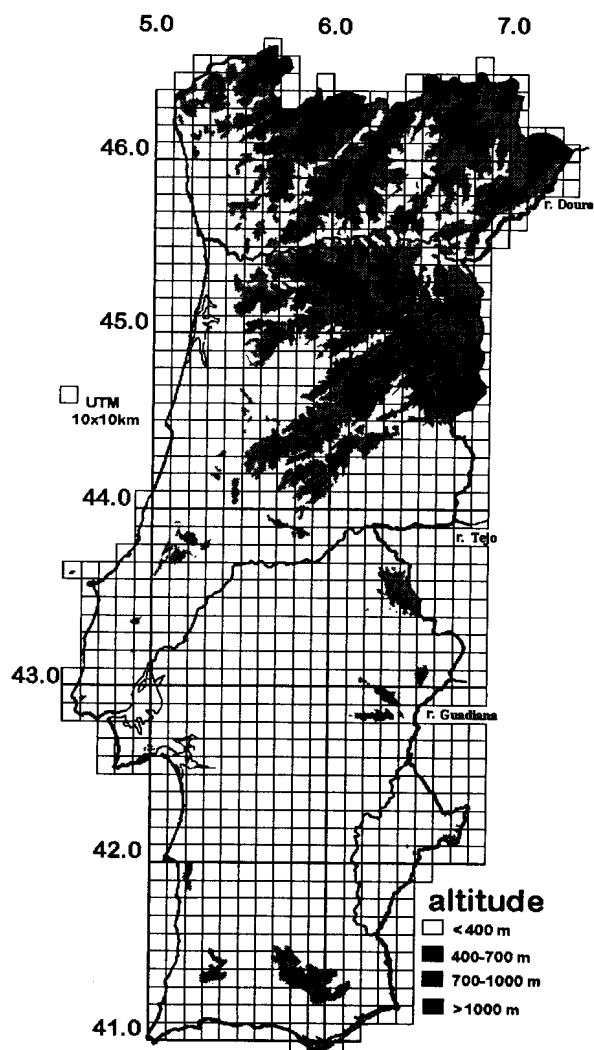
FIG. 3. Altitudinal map of Portugal (adapted from a chart assembled into CNA, 1983).

more variation than other models tested, showing higher values of *G* but fewer variables (all with significant association), while both agreed closely with the observed values. Pearson chi-square values were significant (*P*<0.001) and classification table cases correctly classified over 80% of presence, absence and total records, indicating that both final models are good predictors of the distribution of *P. hispanicus* (Table 1). However, as the predictive models are based on broad-scale environmental data, only general patterns should be obtained from them.

The probability of occurrence of *P. hispanicus* 1 in Portugal is shown in Fig. 1. The likely presence contour (*P*>0.8) broadly matches the known range of this lizard (i.e. northern, central and eastern Portugal), except for the Beira Serra region where no records are available. However, the predictable presence contour (*P*=[0.5-0.8]) extends beyond the known range (e.g. some hilly and mountain areas isolated in western and southern Portugal). Some classes of the environmental variables

such as *altitude* $\geq$400-500 m (Fig. 3), *temperature* $\leq$12.5-15.0°C, *frost* I $\geq$20-30 days and *precipitation* $\geq$700-800 mm often determined the minimum probability for supporting presence in the *P. hispanicus* 1 model.

The probability of occurrence of *P. hispanicus* 2 in Portugal is shown in Fig. 2. The likely presence contour extends further than the known range (e.g. Alto Douro - the upper valley of the river Douro basin; Beira Baixa - the frontier region near the river Tejo). Various peripheral records are not covered even by the contour *P*=[0.5-0.8]. *P. hispanicus* 2 only occurs below the river Douro i.e. south and west-central Portugal. In the model, *altitude* $\leq$300-400 m (see Fig. 3), *temperature* $\geq$15.0-16.0°C, *precipitation* $\leq$600-700 mm and *climate* $\leq$50% often contributed to the minimum probability of occurrence *P*>0.5.

GENERAL DISTRIBUTION PATTERNS

In brief, five general environmental characteristics may be obtained from the models. (1) *P. hispanicus* 1 predominates in the highlands (>400 m) and where Atlantic and/or Continental conditions, i.e. rainy and temperate, prevail (CNA, 1984*a,b*). (2) In contrast, *P. hispanicus* 2 seems to prefer the lowlands (<400 m) and areas where Mediterranean conditions predominate, in Portugal. (3) The altitudinal variation clearly reflects a more complex set of climatic variables that are interacting (Brown & Gibson, 1983; Cox & Moore, 1993). As a consequence, moderate correlation between environmental variables (Pearson's *r*>0.65) was found in the final models: positive for *precipitation* vs. *climate*; and negative for both *altitude* vs. *temperature* and *temperature* vs. *climate* (Table 2). On average, when altitude increases by 100 m, temperature decreases by 0.6° C in Portugal (Albuquerque, 1954). (4) The spatial autocorrelation appears not to confound the model results (see significant but lower correlation between SPACE - "space structure" - and each of the environmental distance matrices in Table 3). It should be noticed that correlation between two distance matrices (Table 3) is not equivalent to correlation between the two environmental variables underlying these matrices (Table 2); a distance matrix correlation measures the extent to which the variations in the "distances" of one matrix correspond to the variations in another (Legendre, 1993). (5) The environmental variables used for the models were included because of their likely biological significance, but the final set of model predictions was largely derived on statistical grounds. Subsequent relationships between lizard distribution and specific environmental variables cannot be assumed to imply causal effect. Although macroenvironmental factors may play an important role, they are obviously not the only factors determining *P. hispanicus'* distribution. For example, other habitat features may be unsuitable in areas which are climatically ideal for certain *P. hispanicus* forms.

TABLE 1. Two best-fit models found for each *P. hispanicus* form and associated statistics: maximum likelihood ratio G; χ^2 and classification tables (P-*P* means observed versus predicted presences, etc.). 100 x temperature/precipitation = K corresponds to Emberger's pluviothermic coefficient (used in climatology), which increases with aridity. *** $P<0.001$.

logistic regression equations	max. likelihood ratio test	validation tests on the sub-samples			
		n	model	n	validation
P. hispanicus 1					
First model:	$G=225.5$***	109	P-*P*: 92.7%	31	P-*P*: 80.6%
Y1=0.2266 $(altitude)^{0.5}$ - 0.03188 $(temperature)^2$		112	A-*A*: 94.6%	27	A-*A*: 100%
-3.1939 (100 x $temperature/precipitation)^{0.5}$ +		221	T-*T*: 93.7%	58	T-*T*: 89.7%
0.09677$(frost$ I) + 3.998		221	χ^2=88.6***	58	χ^2=18.2***
Second model:		109	P-*P*: 88.9%	31	P-*P*: 80.6%
Y2=0.2204 $(altitude)^{0.5}$ - 0.04456 $(temperature)^2$	$G=205.4$***	112	A-*A*: 94.6%	27	A-*A*: 100%
+0.08341$(frost$ I) + 3.021		221	T-*T*: 91.8%	58	T-*T*: 89.6%
		221	χ^2=88.7***	58	χ^2=20.3***
P. hispanicus 2					
First model:					
Y1=0.7782$(temperature)$ - 0.008195$(altitude)$	$G=248.5$***	112	P-*P*: 92.9%	27	P-*P*: 88.9%
-0.0003807$(precipitation)$ x log$(precipitation)$		151	A-*A*: 95.4%	43	A-*A*: 90.7%
-0.0007938$(climate)^2$ - 5.538		263	T-*T*: 94.3%	70	T-*T*: 90.0%
		263	χ^2=108.8	70	χ^2=20.7
Second model:					
Y2=1.268$(temperature)$ - 0.9493(100 x	$G=256.4$***	112	P-*P*: 93.7%	27	P(27)-*P*: 85.2%
$temperature/precipitation)^{0.5}$ - 0.001788		151	A-*A*: 95.4%	43	A(43)-*A*: 95.3%
$(precipitation)$ x log$(precipitation)$ -		263	T-*T*: 94.7%	70	T(70)-*T*: 91.4%
0.008683$(altitude)$ - 0.0008381$(climate)$ -		263	χ^2=116.6***	70	χ^2=21.1***
0.0008381$(climate)^2$ - 3.302					

BIOGEOGRAPHY

Historical factors could have played an important role in determining present-day distributions (Wiens, 1989; Antúnez & Mendoza, 1992), but this remains rather speculative. Two related explanatory hypotheses, which differ in the space-time scale, are discussed here: (1) post-glacial range expansion, such as found for many European fauna (Brown & Gibson, 1983; Cox & Moore, 1993); and (2) formation of a contact zone between two subspecies (Mayr & Ashlock, 1991).

Barbadillo (1987) explains that there are two possible sources of origin for the *P. hispanicus* species as a whole taxon: an Iberian origin from stock related to *P. muralis*, or a Maghrebian origin from stock of an ancient *Podarcis* form. In my opinion, both hypotheses constitute interesting arguments when they are viewed

TABLE 2. Simple normalized Mantel test of matrix correspondence between SPACE distance matrix (i.e. spatial structure) and each environmental distance matrix, after 200 repeated random permutations (* $P<0.005$, one-tailed Mantel test,).

Environmental matrices	Space matrix	
	P. h. 1	*P. h.* 2
n	221	263
altitude	0.29275*	0.18848*
temperature	0.32812*	0.28594*
precipitation	0.27666*	0.33382*
frost I	0.23776*	-
climate	-	0.46456*

TABLE 3. Pearson product-moment correlation between pair(s) of environmental variables: positive values means that both variables tend to increase together; negative values that one variable tends to decrease while the other increases. * $P<0.005$.

	altitude	temp.	precipitation	climate
altitude	-	-0.689*	0.394*	0.407*
temperature	-0.738	-	-0.609*	-0.679*
precipitation	0.482*	-0.611*	-	0.655*
frost I	0.451*	-0.371*	0.690	-

Serra do Arestal; Corga / Bolfiar UTM 44.9 5.5 in the Serra do Caramulo; Castelo de Vide / Carreiras UTM 43.6 6.3 in the Serra de São Mamede); (3) permanent morphological and ecological distinctness is maintained by both *P. hispanicus* 1 and *P. hispanicus* 2 throughout their ranges; and (4) only one example from Marvão showed an intermediate pattern between *P. hispanicus* 1 and *P. hispanicus* 2.

CONCLUSION

Future research should aim at improving the model by incorporating other relevant variables, such as descriptors of habitat quality. The results could also be improved either by changing the scale to a more precise one or by using different modelling approaches e.g. trend surface models and Bayesian integrated statistical inference (Pereira & Itami, 1991). The probability maps also give some useful clues for further surveys on the distribution gaps of this species. It would also be interesting to study (at a fine scale) the contact zone between *P. hispanicus* 1 and *P. hispanicus* 2, examining possible clinal separation or more categorical spatial exclusion, as the first data suggested. For example, García-París, Martín, Dorda & Esteban (1989) found in the Autonomous Community of Madrid (Spain) that either the morphological features, the ecological preferences or the distribution ranges of *P. hispanicus* seem to be related to different geographical areas of that region. Both *P. hispanicus* 1 and *P. hispanicus* 2 morphotypes, and their preferential habitats are described by these authors. It is possible that other potential contact zones, similar to that observed in Portugal, occur elsewhere in Iberia.

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APPENDIX 1

Classes of the five environmental variables used in the final logistic regression equations. Type of climate is a qualitative variable assessed as composition and intergradation (*) of greater climate domains: M, Mediterranean; A, Atlantic; Ã, Atlantic or Macronesian; I, Iberian or continental. S and O refer to the prefixes sub- and oro- respectively, indicating altitudinal effects on climate. *Climate* was extrapolated from the type of climate using the correspondence values (original values emboldened), see Albuquerque (1954) for more details.

class	altitude (m)	temperature (oC)	frost I (days/yr)	rainfall (mm/yr)	climate type	ΣA%
1	<100	<7.5	<1	<400	M	1
2	100-200	7.5-10.0	1-5	400-500	IM*M	7
3	200-300	10.0-12.5	5-10	500-600	IM	13
4	300-400	12.5-15.0	10-20	600-700	SM*IM	17
5	400-500	15.0-16.0	20-30	700-800	SM	**20**
6	500-600	16.0-17.5	30-40	800-1000	AM*SM	**30**
7	600-700	>17.5	40-50	1000-1200	ÃM*SM	32
8	700-800		50-60	1200-1400	SA*SM*IM	34
9	800-900		60-70	1400-1600	ÃM	37
10	900-1000		70-80	1600-2000	AM	**40**
11	1000-1100		>80	2000-2400	SA*I	45
12	1100-1200			2400-2800	MA*AM	**50**
13	1200-1300			>2800	SA*SM	54
14	1300-1400				MA	**60**
15	1400-1500				SA*AM	65
16	1500-1600				SÃ*SM	66
17	1600-1700				SA*MA*AM	67
18	1700-1800				SA*MA	69
19	>1800				A*MA	**70**
20					SA*A*MA	71
21					SA	73
22					SÃ	75
23					A*SA	**80**
24					OA*SA or OA	85