

DISTRIBUTIONAL ANALYSIS OF TWO VIPERS (*VIPERA LATASTEI* AND *V. SEOANEI*) IN A POTENTIAL AREA OF SYMPATRY IN THE NORTHWESTERN IBERIAN PENINSULA

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ABSTRACT: A logistic regression was used to model the distribution of Lataste's Viper (*Vipera latastei*) and Iberian Adder (*V. seoanei*) in a potential area of sympatry in the northwestern region of the Iberian Peninsula. The model was based on biogeophysical variables such as rainfall, elevation, and vegetation, and predicts the probability of occurrence at a 1 x 1 km scale. The analysis was performed using Geographic Information Systems (GIS). We checked for spatial autocorrelation of data, and models gave correct classification rates above 95%. We found that variables explaining distribution in both species were similar but with opposite coefficient signs, meaning that what one species prefers the other avoids. We therefore developed a single model for both species. The model demonstrates that compared to *V. seoanei*, *V. latastei* prefers lower elevations, higher insolation, higher precipitation, more rock outcrops, less bushy vegetation, and areas without brooms (*Cytisus* sp.). We discuss the significance of these biogeophysical variables in explaining the distribution of both species and compare our results with examples of sympatry among other species of vipers. Although co-existence in the field between *V. latastei* and *V. seoanei* was not detected, the model delimits an area of probable sympatry at a 1 x 1 km scale. We suggest that the lack of absolute sympatry at this scale may be the consequence of interspecific competition or differential habitat preferences, but more data are needed to draw firm conclusions.

INTRODUCTION

The distribution of most species of European vipers is parapatric (Gasc et al., 1997), and thus they usually do not overlap except in specific areas (Saint Girons, 1980). Sympatry, for example, has been detected in *Vipera aspis* and *V. berus* in the pre-Alps of western Switzerland (Monney, 1994) and the region of Nantes in western France (Naulleau, 1986). Additionally, sympatry occurs in *V. aspis* and *V. latastei* in the southern Pyrenees (Saint Girons, 1980) and the Spanish Basque country (Bea, 1985). Although these areas have been characterized in terms of vegetation and climate, it is not clear what factors determine the distribution of these species. Accordingly, modeling the distribution of European vipers in relation to biogeophysical variables has the potential to offer insights in explaining sympatry and other distributional phenomena.

Our objective in this study was to model the distribution of Lataste's Viper (*Vipera latastei* Boscá, 1878) and Iberian Adder (*V. seoanei* Lataste, 1879) in the northwestern region of the Iberian Peninsula, and to identify factors that affect the distribution of both species. *Vipera latastei* occurs throughout most of the Iberian Peninsula, whereas *V. seoanei* is restricted to the septentrional area of the peninsula (Fig. 1). Our study was conducted in an area of potential sympatry for both species, and this is the northern distributional limit for *V. latastei* and the southern one for *V. seoanei* (Godinho et al., 1999).

Logistic regression was used to model the distribution of both species, as it has proven to be a tool capable of analyzing the effects of one or several independent variables, discrete or continuous, over dichotomic (presence/absence) or polychotomic dependent variables (Brito et al, 1999). This modeling technique has been improved with integration of Geographic Information Systems (GIS), as it provides the ability to store, display, and analyze spatial data. Moreover, GIS can be used to derive predictive models from relationships between the data, and extrapolate the potential distribution, abundance, or habitat preferences of a species from those models (e.g., Haslett, 1990).

METHODS

Study Area

The study area encompassed 1,974 km² and is located in the northwestern region of the Iberian Peninsula along the border between Portugal and Spain (lat. 41°36' to 42°07' N, long. 7°44' to 8°27' E; Fig. 1). Most of the area lies in two protected parks, Peneda-Gerês National Park (Portugal) and Baixa Limia-S. Xurés Natural Park (Spain). The area is a granitic mountain ranging in elevation from 50 to 1,500 m. The climate is characterized as a transition between Atlantic Mediterranean and Continental Mediterranean (Goday, 1951–53), with high levels of precipitation (average annual rainfall > 3,000mm). Vegetation consists primarily of deciduous oak forest (*Quercus robur* and *Q. pyrenaica*) or mixed deciduous and coniferous forest. Major shrubs are heath (*Erica* sp.), furze (*Ulex* sp.), and brooms (*Cytisus* sp.).

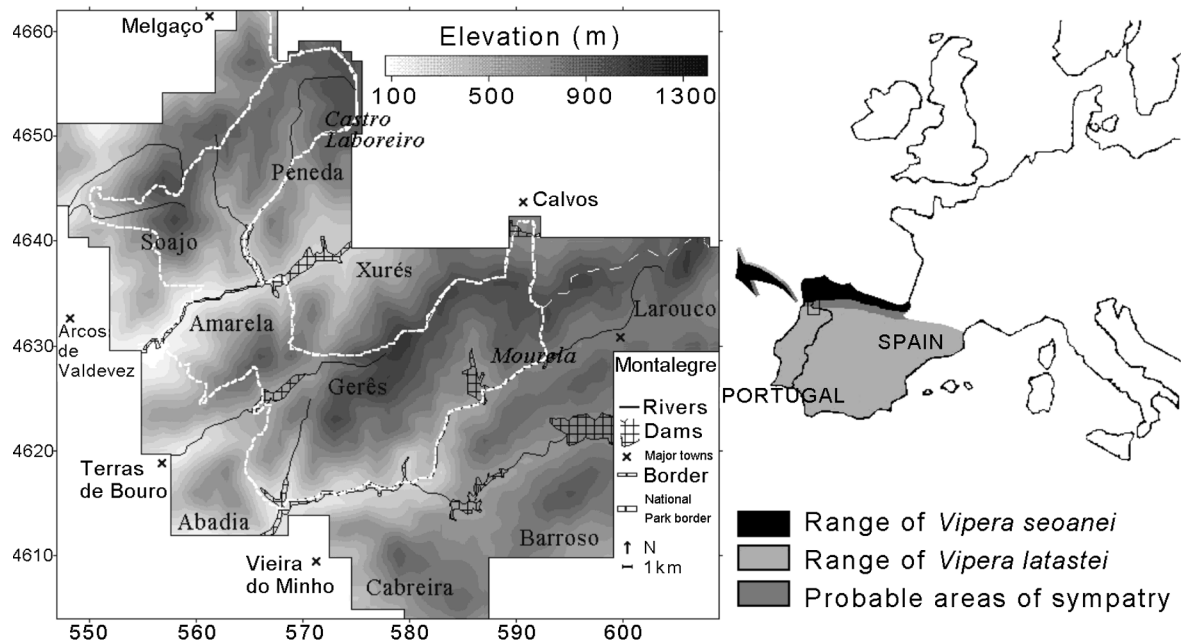


Fig. 1. Distribution of *Vipera latastei* and *Vipera seoanei* in the Iberian Peninsula (right) and map of the study area (left). Gray scale denotes elevation, the names depicted are for mountains, and mountain plateaus are in italics.

Data Collection

From 1993 to 1999, 79 observations of *V. latastei* and 34 observations of *V. seoanei* were made in UTM (Universal Transverse of Mercator) 1 x 1 km squares (Fig. 2). Observations consisted of live and road-killed snakes. Data were not collected randomly as the concentration of observations of *V. latastei* in the western Gerês Mountain resulted from the location of the Peneda-Gerês National Park headquarters, where forest rangers frequently found and reported their observations on road-killed specimens.

Two matrices (*V. latastei*: *V. seoanei*) were built, in which the absence or presence (0/1) of the species (dependent variable) was recorded in UTM 1 x 1 km squares (single-species models). A third matrix gathered all the data (two-species model) with 79 presences of *V. latastei* (value 1) and 34 presences of *V. seoanei* (value 0). The UTM 1 x 1 km squares were characterized with 47 independent variables (Table 1).

Spatial Autocorrelation

Because neighboring squares of the 1 x 1 km grid tend to have similar environmental and biological conditions, spatial autocorrelation may result. Spatial autocorrelation reduces the number of independent observations, which in turn may reduce the power of the model (Anselin, 1993; Augustin et al., 1996). In order to measure spatial autocorrelation of the depen-

dent variable, we calculated Moran's I (Cliff and Ord, 1973), using the AUTOCORR procedure of the IDRISI for Windows (Eastman, 1995) GIS package. We used the Queen's case type of spatial autocorrelation, which tests if squares with determined values have a common edge and/or vertex (Cliff and Ord, 1973). Values of Moran's I range between -1 and +1. Values approaching +1 indicate a smooth surface, with each square containing values similar to the neighboring ones, and values approaching -1 indicate rough or fractured surfaces, with adjacent squares of different values (Eastman, 1995). The AUTOCORR procedure measures spatial autocorrelation for adjacent neighbors of a square, called first lag, and for subsequent lags increasing distance neighbors (Eastman 1995), allowing us to construct correlograms. These correlograms relate the level of spatial autocorrelation with increasing distances and determine the distance beyond which spatial autocorrelation has no further effect on the data (Kintorn et al., 1996).

The level of spatial autocorrelation is small, using all information (0 km distance) for both *V. latastei* (0.30) and *V. seoanei* (0.23) (Fig. 3). When the information from neighboring squares (1 or 2 km distance) is not used, Moran's I will decrease, but this leads to a smaller number of available squares to build the models. Thus, we decided to use all information (0 km distance).

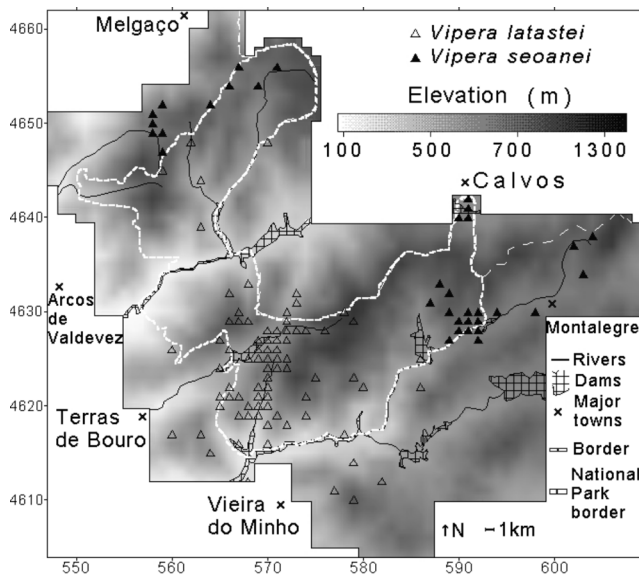


Fig. 2. Distribution of *Vipera latastei* and *Vipera seoanei* in the study area. Each triangle represents an observation in a 1 x 1 km UTM square. Gray scale denotes elevation.

Model Building

The models were built with SPSS software (Norusis, 1995) following the procedures recommended by Hosmer and Lemeshow (1989) and Brito et al. (1999). We checked for correlations between independent variables. For pairs of variables with correlation above 0.500, we eliminated the ones that were weaker descriptors of the presence of the species. From the 47 initial variables we excluded 10 because they had correlation levels with other variables above 0.500 in the Pearson correlation coefficient (Tab. 2).

Statistics of each variable were examined by performing a univariate analysis; correspondingly, we present the level of significance for the Wald test (Table 3). From the 37 variables used in this analysis we excluded 24 variables in the model for *V. latastei*, 22 variables in the model for *V. seoanei*, and 21 variables in the two-species model. From the variables excluded, 20 are common for the three models.

A multivariate analysis was performed and the variables were ranked according to the resulting statistics of these two steps. A backwards stepwise elimination process was performed. The variables with $P > 0.01$ in the Wald test, or those that did not significantly contribute to the model estimated by the G test were removed. The variables considered relevant during the multivariate analysis were tested for linearity. This procedure was performed with a univariate analysis of the transformed variable in x^2 , $\log(x)$ and $x \cdot \log(x)$. If any transformation increased the predictive power of

the model it was retained and the non-transformed variable was removed. The linearity test yielded significant transformations of logarithm of FRO and the square of ERI in the model for *V. latastei*, while in the model for *V. seoanei* there was no significant transformation. In the two-species model the only variable to be transformed was $\log(\text{FRO})$, but it was later removed due to unstable coefficient estimates.

Because there is always some degree of correlation between the independent variables, we checked for possible interaction between variables by adding the term $x \cdot y$, x and y being two different variables in the model. If the power of the model increased substantially by adding the interaction, then the interaction was retained. In the model for *V. seoanei* and in the two-species model there was no significant interaction between variables, while in the model for *V. latastei* there was one, $\text{TBU} \times (\text{ERI})^2$, although it was later removed due to unstable coefficient estimates.

Last, we tested the final model by adding the variables Northing and Easting, and checked for significant coefficients. Since these variables by themselves are not expected to have a significant influence in the distribution of species (Gates et al., 1994), significant coefficients act as substitutes for more important variables. The introduction of the variables Northing and Easting yielded no significant results in any of the three models.

To access the accuracy of the models we used correct classification rates (1) and statistical tests (2). The model classifies squares with a continuous value for probability of occurrence between 0.0 and 1.0. Defining a cut-off point above which we consider the species present, we can detect if the model correctly classifies a square with presence or absence. During

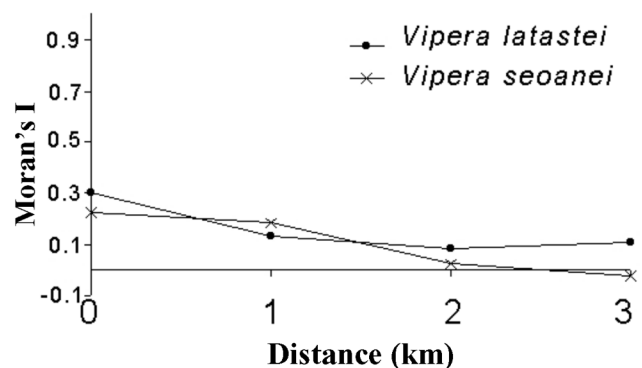


Fig. 3. Spatial autocorrelation of *Vipera latastei* and *Vipera seoanei* observations measured by Moran's I in relation to distance.

Table 1. Independent variables used to characterize the UTM 1x1 km squares. PEA = Portuguese Environmental Atlas (C. N. A., 1983). MM = military maps at 1:25.000 scale. FW = fieldwork (this study).

Variable	Code	Source	Unit
Average elevation	AAV	MM	m a.s.l.
Maximum elevation	AMA	MM	m a.s.l.
Minimum elevation	AMI	MM	m a.s.l.
Slope	SLO	MM	%
Orientation	ORI	MM	
Dominant type of soil	SOI	PEA	
Total annual precipitation	PRE	PEA	mm/year
Average annual insolation	INS	PEA	N hours/year
Average annual soil draining	DRA	PEA	mm/year
Average annual evapotranspiration	EVA	PEA	mm/year
Average annual air temperature	TEM	PEA	°C/year
Average air humidity	HUM	PEA	% at 9:00 GMT
Average number of days per year with fog	FOG	PEA	N days/year
Average number of days per year with frost	FRO	PEA	N days/year
Average solar radiation	RAD	PEA	kcal/cm ²
Phyto-edapho-climatic information	ECO	PEA	
Number of water courses	NWC	MM	
Largest water course	BWC	MM	
Number of water masses	NWM	MM	
Largest water mass	BWM	MM	
Amount of stone walls	STO	MM	m
Area of rock outcrops	ROC	FW	%
Area of agricultural areas	AGR	FW	%
Area of pastures with stone walls	PAS	FW	%
Area occupied by bushes	BUS	FW	%
% of bushes dominated by furze (<i>Ulex</i> sp.)	ULE	FW	%
% of bushes dominated by heath (<i>Erica</i> sp.)	ERI	FW	%
% of bushes dominated by broom (<i>Cytisus</i> sp.)	GEN	FW	%
% of bushes dominated by high altitude dwarf-shrubs	ALS	FW	%
% of trees dominated by deciduous oaks (<i>Quercus robur</i> and <i>Q. pyrenaica</i>)	DOA	FW	%
% of trees dominated by birches (<i>Betula</i> sp.)	BET	FW	%
% of trees dominated by arbutus-trees (<i>Arbutus unedo</i>)	ARB	FW	%
% of trees dominated by pines (<i>Pinus</i> sp.)	PIN	FW	%
% of trees dominated by eucalyptus (<i>Eucalyptus</i> sp.)	EUC	FW	%
% of trees dominated by ever-green oaks (<i>Q. suber</i> and <i>Q. ilex</i>)	GOA	FW	%
% of trees dominated by acacias (<i>Acacia</i> sp.)	ACA	FW	%
% of trees dominated by conifers (<i>Cupressus</i> sp. and <i>Chamaecyparis</i> sp.)	COM	FW	%
Area occupied by thick arboreous strata	TTR	MM	%
Area occupied by scattered arboreous strata	STR	MM	%
Area occupied by thick arbustive strata	TBU	MM	%
Diversity of plant species in the arbustive strata	DBU	FW	
Diversity of plant species in the arboreuos strata	DTR	FW	
Intensity of human buildings	MAN	MM	
Amount of paved road	RPA	MM	m
Amount of unpaved road	RUN	MM	m
Largest road	BRO	MM	
Area occupied by dams	DAM	MM	%

Table 2. Independent variables eliminated due to high levels of correlation. Correlation significant at $P = 0.01$.

Eliminated variables	Pearson's correlation coefficient
AAV	0.935
AMA	0.830
ECO	− 0.638
NWM	0.593
BWM	0.721
PIN	− 0.527
DTR	0.596
MAN	0.673
RPA	0.699
RUN	− 0.814

this analysis we ran the model with all cut-off points between 0.0 and 1.0, with intervals of 0.1, and obtained correct classification rates for presences, absences, and combination of both (1). As a statistical test (2), we used the Pearson χ^2 which measures the accuracy of the model in terms of confronting the probability for the species to be present in a given square with the real presence or absence of the species for that square. If the model gives a high probability of occurrence for a square (e.g., 0.8) and the species is absent, or the inverse by giving a small probability of occurrence (e.g. 0.2) for a square where the species is

Table 3. Significance of Wald test obtained during univariate analysis for *Vipera latastei*, *Vipera seoanei*, and two-species models. Variables marked with * were eliminated.

Variable	<i>Vipera latastei</i> model	<i>Vipera seoanei</i> model	Two-species model
AMI	0.0000	0.0000	0.0000
SLO	0.0000	0.0000	0.0000
ORI	0.0054*	0.8054*	0.4967*
SOI	0.3998*	0.0029*	0.0133*
PRE	0.0000	0.0000	0.0000
INS	0.0003	0.0002	0.0000
DRA	0.0000	0.0000	0.0000
EVA	0.2073*	0.7938*	0.7998*
TEM	0.9345*	0.6274*	0.5827*
HUM	0.0000	0.0000	0.0000
FOG	0.0000	0.0003	0.0000
FRO	0.0000	0.0000	0.0000
RAD	0.5991*	0.7034*	0.6912*
NWC	0.0000	0.0115*	0.0096*
BWC	0.0999*	0.4313*	0.3414*
ROC	0.0000	0.0000	0.0000
AGR	0.0013*	0.0001	0.0000
PAS	0.0000	0.0001	0.0000
STO	0.0026*	0.0017	0.0001
BUS	0.0206*	0.4507*	0.4589*
ULE	0.2159*	0.2902*	0.7415*
ERI	0.0000	0.0000	0.0000
GEN	0.0000	0.0000	0.0000
ALS	0.0005*	0.2864*	0.1143*
DOA	0.0254*	0.0021	0.0010
BET	0.4450*	0.8933*	0.6762*
ARB	0.6765*	0.7920*	0.7393*
EUC	0.6220*	0.7460*	0.6948*
GOA	0.6765*	0.7938*	0.7393*
ACA	0.5796*	0.7019*	0.7528*
CON	0.4278*	1.0000*	0.9370*
TTR	0.0010*	0.0909*	0.0603*
STR	0.0250*	0.0926*	0.1815*
TBU	0.0000	0.0004	0.0000
DBU	0.8965*	0.2877*	0.3345*
BRO	0.3766*	0.0052*	0.0107*
DAM	0.0744*	0.7710*	0.7822*

Table 4. Variables included in the regression equations of the models for *Vipera latastei*, *Vipera seoanei*, and the two-species model.

<i>Vipera latastei</i> model					
Variable	Coefficient	Wald test	Significance	G test	Pearson χ^2
Minimum elevation	– 0.0123	13.3394	0.0003	229.066	83.235
Average annual insolation	0.0102	7.9185	0.0049		df = 192
Area occupied by bushes	– 1.2126	3.8755	0.0490		
Average annual precipitation	0.0077	11.3691	0.0007		
Area of rock outcrops	1.6151	9.0606	0.0026		
Constant	– 31.1114	7.7051	0.0055		
<i>Vipera seoanei</i> model					
Variable	Coefficient	Wald test	Significance	G test	Pearson χ^2
Minimum elevation	0.0161	10.2709	0.0014	91.065	45.359
Area of rock outcrops	– 1.9651	10.2704	0.0014		df = 81
Average annual precipitation	– 0.0028	3.3753	0.0662		
Constant	– 4.7835	1.2203	0.2693		
Two-species model					
Variable	Coefficient	Wald test	Significance	G test	Pearson χ^2
Minimum elevation	– 0.0148	4.6566	0.0309	125.341	15.101
Average annual insolation	0.0095	2.0547	0.1517		df = 106
Area occupied by bushes	– 2.2110	1.7964	0.1801		
Average annual precipitation	0.0063	2.5405	0.1110		
Area of rock outcrops	2.9848	2.9773	0.0844		
% of bushes dominated by brooms (<i>Cytisus</i> sp.)	– 1.0604	2.6130	0.1060		
Constant	– 23.2215	1.3414	0.2468		

present, the model does not fit the data. The value of X^2 is obtained by:

$$\sum_{j=1}^n r(y_j, \pi_j)^2, \text{ where } r(y_j, \pi_j) = \frac{(y_j - \pi_j)}{\sqrt{\pi_j(1 - \pi_j)}}$$

The term π_j is the probability of occurrence of the species in a given square (ranging from 0.0 to 1.0), and y_j is the real data, 0 if the species is absent, or 1 if the species is present. The Pearson chi-square follows the normal distribution of a chi-square test with the null hypothesis that the model fits the original data. The greater the difference between the X^2 and the χ^2 denotes that the model better fits the data. For model output, we used SIG Surfer for Windows ver. 6.04 (Keckler, 1996). The final outputs were maps with probability of occurrence for *V. latastei* and *V. seoanei* in the study area.

RESULTS

We present in Table 4 the final models for *V. latastei*, *V. seoanei*, and the two-species model after

the backwards elimination process. We did not reject the null hypothesis that the model fits the data ($P = 0.001$) for any of the three models. In Figure 4 we present the correct classification rates for the presence, absence, and a combination of both. In all the cases, the cut-off point that produces the most correct classification rate of the presences is 0.4 and correct classification is always above 95%. Although the cut-off point that optimizes the three rates is 0.5, under these circumstances it is better to have higher rates in the correct presences classification, because the absence may not correspond to a real absence but caused by the non-detection of the species in a certain square, where it actually existed.

The results of the single-species models suggest that biophysical variables (climate: precipitation and insolation), physical (minimum elevation) and habitat (amount of rock outcrops and thick bushes) influences the distribution of the snakes. Nevertheless, the most interesting fact is the presence of three variables in both models, but with opposite signs in the coefficients. The coefficients are also of the same magni-

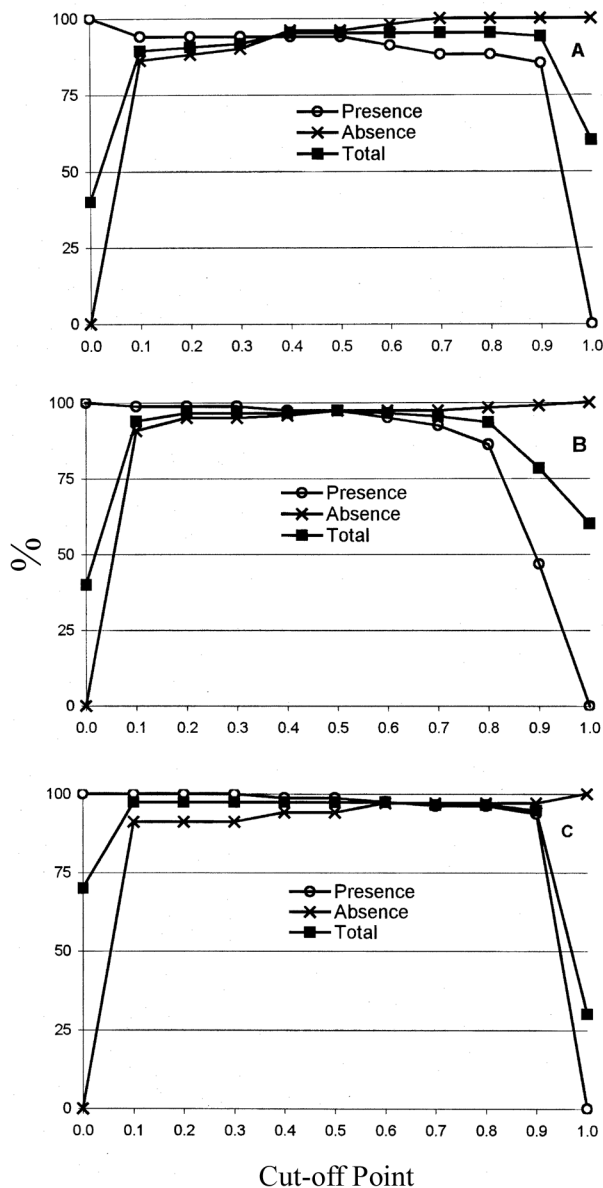


Fig. 4. Correct classification rates of the models for (A) *Vipera latastei*, (B) *Vipera seoanei*, and (C) the two-species model considering all possible cut-off points at 0.1 intervals.

tude, meaning that that *V. latastei* prefers lower elevations (negative sign in the coefficient) than *V. seoanei* (positive sign in the coefficient). Compared with *V. seoanei*, *V. latastei* is found in areas with higher rainfall and with more rock outcrops. These results are a consequence of parapatric distribution in both species. Whenever one species is present in a certain location the other is absent the same variables, but with different trends, explain the distribution of both species.

The results of the two-species model are similar to the previous single-species models. Again, this model suggests that compared with *V. seoanei*, *V. latastei*

occurs in areas of low elevation, higher insolation, higher precipitation, more rock outcrops and less bushy vegetation. The only new variable is the percentage of bushes dominated by brooms (*Cytisus* sp.) favored by *V. seoanei*.

In Figures 5–7 we present the occurrence probability of *V. latastei*, *V. seoanei* and both species, respectively, determined by their respective models. The more obvious result presented in the single-species occurrence probability maps (Figs. 5–6) is that potential areas of occurrence complement each other. In the map with occurrence probability combined for both species (Fig. 7), we see that the areas with greater probability for finding *V. latastei* are the mountains of Gerês, Xurés, Amarela, Peneda, Abadia, and the south- and west-facing slopes of Soajo Mountain (Fig. 1). *Vipera seoanei* potentially occupies all of the Castro Laboreiro and Mourela plateaus, the north facing slope of Soajo Mountain, and Larouco Mountain. Few observations have been made in the mountains of Cabreira and Barroso, and those areas will require further sampling.

According to the model, probable areas of sympatry include the transition zone between Gerês Mountain and Mourela plateau, all of Soajo Mountain, and the area between Peneda Mountain and Castro Laboreiro plateau. In the Barroso and Cabreira mountains additional data are needed to draw firm conclusions.

DISCUSSION

Vipera latastei has been reported to inhabit dry, rocky or sandy areas, covered or surrounded by open vegetation and adequate conditions for insolation, whereas *V. seoanei* is not found in regions with a Mediterranean climate, but occupies moist and wet habitats with dense vegetation (Saint Girons, 1980; Gasc et al., 1997; Nilson and Andrén, 1997). The data from our models supports these statements. A variable from our model that has not been reported is the percentage of bushes dominated by brooms. In our study area, however, brooms are more common in colder regions, which coincides with areas where *V. seoanei* is present, and this variable explains the distribution of both species.

In areas of potential sympatry between *V. latastei* and *V. aspis* south of the Pyrenees (Saint Girons, 1980), and between *V. seoanei* and *V. aspis* in the Spanish Basc Country (Bea, 1985), the importance of climate and topography has been discussed. In the Pyrenees, this type of distribution occurs in an area of dozens of kilometres, between 400 m and 1,200 m

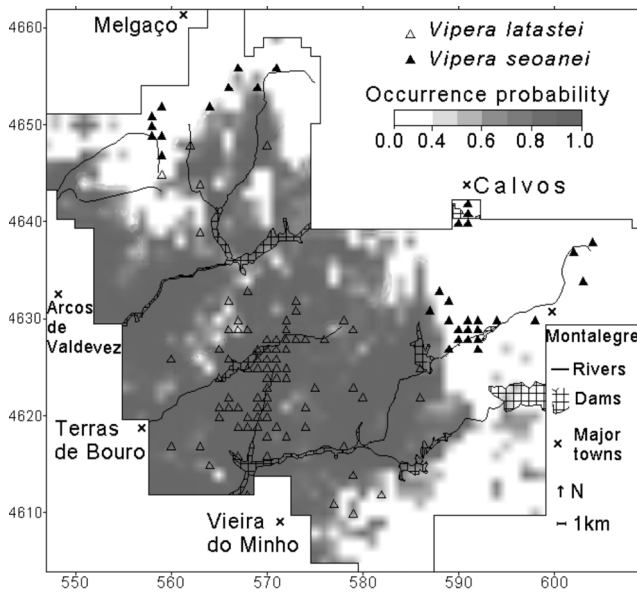


Fig. 5. Occurrence probability of *Vipera latastei* according to the logistic regression model in the study area (cut-off point 0.4).

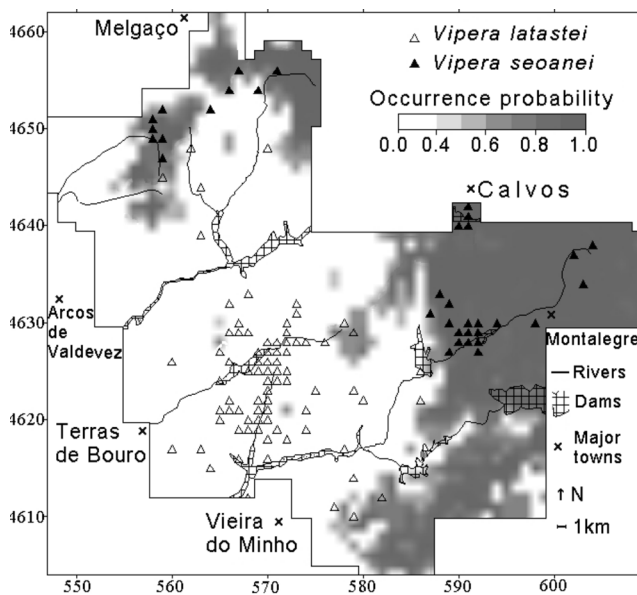


Fig. 6. Occurrence probability of *Vipera seoanei* according to the logistic regression model in the study area (cut-off point 0.4).

(Saint Girons, 1980). In this region, *V. latastei* occupies the warmer, drier, south-facing slopes, while *V. aspis* is found in the more humid north-facing slopes. According to Bea (1985), in the Spanish Basque Country *V. seoanei* occupies humid and cooler areas with abundant Atlantic vegetation (deciduous oaks, *Q. robur* and *Q. pyrenaica*) in the lower, north-facing valleys, while *V. aspis* is found in drier areas with Mediterranean-Continental vegetation (evergreen oaks, *Q. suber* and *Q. ilex*) in smooth north- or south-

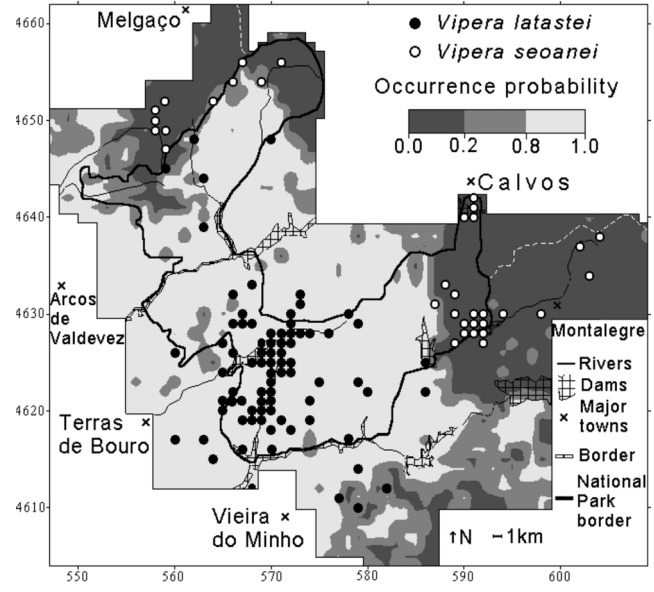


Fig. 7. Occurrence probability of *Vipera latastei* and *Vipera seoanei* in the study area according to the logistic regression model. In areas with an occurrence probability lower than 0.2 *Vipera seoanei* is most likely to be found, and above 0.8 it will likely be *Vipera latastei*. In areas where the occurrence probability is between 0.2 and 0.8, either species could be present.

facing slopes. Similar situations occur with other European vipers, e.g., between *V. aspis* and *V. berus* in the pre-Alps (Monney, 1994) and in the region of Nantes (Naulleau, 1986). In these areas *V. aspis* consistently occupies the warmer and drier south-facing slopes, and *V. berus* occurs on north-facing slopes.

In our study area, *V. latastei* and *V. seoanei* may co-exist in locations that are less than two km apart (Fig. 2), but a situation of actual sympatry was not detected. A similar situation may occur with *V. aspis* and *V. berus* in the pre-Alps (Monney, 1994), and in the Spanish Basque country with *V. seoanei* and *V. aspis* (Bea, 1995). Hence, we conclude that although these species may occur in nearby locations, and even occupy similar habitats, they may not co-exist. The sympatry issue in European vipers is clearly a matter of scale (Saint Girons, 1980). At a macro-scale, (e.g., the Atlas of Amphibians and Reptiles in Europe; Gasc et al., 1997) which employs a 50 x 50 km scale, we see areas of sympatry between *V. latastei* and *V. seoanei* throughout the northwestern Iberian Peninsula. Even at a 10 x 10 km scale there is a high degree of sympatry between these two species (Godinho et al., 1999), but with a detailed analysis at a micro-scale (e.g., 1 x 1 km) finding both species in the same locality may not be possible. Nevertheless, in our study area, more data are needed for places where the two

species are potentially in contact (Soajo Mountain and the eastern end of Gerês Mountain; Fig. 1).

A possible explanation for a lack of co-existence is interspecific competition based on food limitation. Shine (1977) gives an example how sympatric Australian elapids have a low interspecific dietary overlap, and according to Arnold (1972), sympatric snake species tend to consume different types of prey. Bea and Braña (1988) and Braña et al. (1988) state that *V. latastei* and *V. seoanei* feed mainly on small mammals, and this factor may be partially responsible for the lack of sympatry in the vipers of our study area. The vipers show some degree of difference in prey preference, since *V. latastei* feeds on a wider spectrum of prey items with mammals representing 57.5% of the diet (Bea and Braña, 1988), while *V. seoanei* feeds more exclusively on small mammals (72.0%) (Braña et al., 1988). These data, however, were obtained from individuals collected throughout Spain, and thus regional differences due to local variation in prey availability and abundance are expected. Currently, we are examining the feeding habits of both species and prey availability in our study area to determine any dietary overlap.

A different use of microhabitat may also exist in sympatric snake species; this has been reported for North American pitvipers (Reinert, 1984). Accordingly, in the areas where *V. latastei* and *V. seoanei* are found in sympatry, we are gathering data on the habitat and/or microhabitat to carry out a more detailed analysis to determine any degree of separation caused by a differential habitat use.

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