BIOLOGICAL CONSERVATION 142 (2009) 344–352

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Habitat suitability, threats and conservation of isolated populations of the smooth snake (*Coronella austriaca*) in the southern Iberian Peninsula

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ARTICLE INFO

Article history:
Received 13 February 2008
Received in revised form
13 October 2008
Accepted 19 October 2008
Available online 4 December 2008

Keywords:
Coronella austriaca
ENFA
Habitat-suitability modelling
Iberian Peninsula
Peripheral populations
Predicting occurrence of rare species
Spatial distribution

ABSTRACT

During the Pleistocene, climatic fluctuations due to glacial and interglacial periods greatly modified the distribution of boreal organisms. One direct effect of these distribution shifts is that, along the southern edge of the range of some boreal species, populations persist only in isolated patches of suitable habitats, surrounded by less suitable areas. Isolated populations in marginal habitat are vulnerable to several threats, including climate change, anthropogenic threats, and stochastic events. We developed habitat-suitability models using Ecological Niche Factor Analysis for populations of the smooth snake, *Coronella austriaca*, at the southernmost limit of the species range. These models were based on historical and current records of occurrence, coupled with remote sensing data including elevation, slope, and climatic variables. Our results indicated that *C. austriaca* in the Iberian Peninsula occurred in areas associated with high slope and precipitation, low temperatures, and low variation in seasonal temperature and precipitation compared to areas of non-occurrence. At a broad scale, the areas classified as highly suitable for the species in the southern Iberian Peninsula were small and fragmented. At a local scale, extensive field work demonstrated that *C. austriaca* occurs in low densities in these areas. In addition, we detected several human-induced threats like habitat loss, favoured by temperature increase and rainfall reduction. Several life-history traits, such as dietary specialization and low frequency reproduction, also may contribute to the vulnerability of these populations to local extinctions. Although the most suitable southernmost areas are included in protected reserves, specific guidelines for management are needed to assess conservation needs.

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0006-3207/$ - see front matter
doi:10.1016/j.biocon.2008.10.030

1. Introduction

The sequence of Pleistocene glacial and interglacial periods produced shifts in the geographic distribution of species according to changes in temperature (Coope, 1994; Hewitt, 2000, 2003). In Europe, the southern peninsulas, i.e. Iberian, Italian, and Balkan, served as refugia during cold periods for many species (e.g. Ursenbacher et al., 2005), and in turn were the origins of northwards expansions during warm periods. The role of these southern populations as glacial refugia and in speciation processes due to isolation and genetic drift has been revealed though numerous molecular studies (e.g. Soulé and Khom, 1989; Lesica and Allendorf, 1995; Santos et al., 2008). Thus, their protection may be beneficial to the conservation of evolutionary processes and genetic diversity, and should be the focus of primary conservation management (Frankham et al., 2004).

Reptiles, as ectothermic organisms, are sensitive to temperature oscillations (Pough, 1980). Their persistence during glacial events is therefore likely to have been reliant on refugia. Southern populations of the smooth snake, *Coronella austriaca* Laurenti, 1768, in the Iberian Peninsula provide an interesting example of this phenomenon (Santos et al., 2008). The distribution of this species in the Iberian Peninsula is distinctive, with continuous populations in the north, but small, isolated populations restricted to mountain chains in the central and southern Iberian Peninsula (Galán, 2002). In these montane areas, infrequent reported occurrences suggest low population densities (Galán, 2002). Consequently, these populations may be subjected to higher extinction risks, due to stochastic and human-related factors, than populations in northern Iberian range. The importance of conserving isolated populations of this species has been highlighted by recent research showing high molecular variability and genetic differentiation from populations in the south of the species' range (Santos et al., 2008).

The goal of our research was to assess the conservation status of *C. austriaca* in the southern Iberian Peninsula by combining information obtained in three different ways: (1) intense field work focusing on the southernmost Iberian populations, (2) identification of the main anthropogenic threats to isolated southern populations, and (3) predictive models of *C. austriaca* distribution in the Iberian Peninsula. Ecological modelling is a useful technique to estimate the suitability of areas for rare and endangered species (Guisan et al., 2006), particularly from a conservation perspective (Engler et al., 2004). Combining information on habitat suitability, threats, and population-density estimations of small populations is a useful way to assess the conservation status of rare species, and to promote efficient protection plans.

2. Materials and methods

2.1. Distribution and natural history

The smooth snake, *C. austriaca,* is a small colubrid widely distributed in Europe. *C. austriaca* reaches southern limits in the Italian, Balkan, and Iberian Peninsulas, and also occurs on some Mediterranean islands, such as Sicily (Strijbosch, 1997). In the Iberian Peninsula, *C. austriaca* is found throughout the northern belt, uniformly occupying the Euro-Siberian region. In contrast, in the Mediterranean bioclimatic region *C. austriaca* occurs in very isolated populations (Galán, 2002; Fig. 1). In the north-western Iberian Peninsula, the smooth snake *C. austriaca* inhabits a variety of habitats, and occupies a wide altitudinal range, occurring in high density populations (e.g. 27 individuals in a 100-m transect; Galán and Fernández-Arias, 1993). In contrast, southern Iberian populations inhabit exclusively montane habitats, and appear to exist in low densities (Galán, 2002). *C. austriaca* is very specialized in terms of food requirements, consuming lizards, and sporadically small mammals (Galán, 1998). *C. austriaca* is viviparous, frequently active during the day, but crepuscular in summer.

2.2. Study area and historical records

The focus of this study is centred around the isolated smooth snake *C. austriaca* populations of the southeastern Iberian Peninsula, a region which includes the Betic range (Fig. 1). This is a chain of rugged and isolated mountains (locally called "sierras"), reaching 3481 m in altitude in the Sierra Nevada, and surrounded by wide valleys. In these mountains the climate is moderately wet and cool (mean annual precipitation and temperature between 500 and 1300 mm and 4.2–12.1 °C, respectively; Hijmans et al., 2005). Natural habitats remain relatively undisturbed, and vegetation consists of stunted shrubs and perennial herbs patchily distributed through large extensions of bare soil and rock. In valleys, vegetation has been extensively altered by humans. Currently, small patches of natural Mediterranean forests and

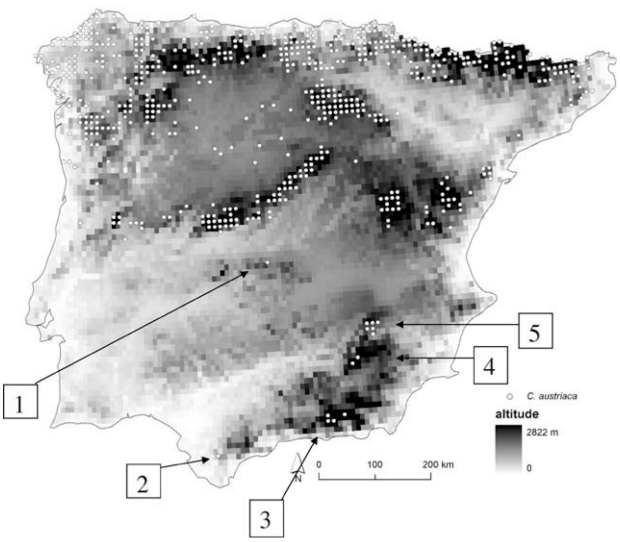

Fig. 1 – Distribution of *Coronella austriaca* in the Iberian Peninsula in UTM 10 × 10 km quadrants. The map is modified from Galán (2002) and overlapped with an altitudinal greyscale grid. Numbers identify known *C. austriaca* localities in central and southern Iberian Peninsula: Montes de Toledo (1), Sierra del Aljibe (2), Sierra Nevada (3), Sierra de Cazorla (4), and Sierra de Alcaraz (5). The latter four mountain ranges from parts of the Betic range.

scrublands remain in valleys, mixed with extensive areas of cultivated cereal cropland and olive plantations.

In the southern Iberian Peninsula, the smooth snake *C. austriaca* has only been found in undisturbed montane habitats at high altitudes (76.4% of 10 × 10 UTM squares with presence above 500 m of altitude). Even in these areas, there are very few records of *C. austriaca* localities: one record in Montes de Toledo (Donaire et al., 2001), one in the Sierra de Cazorla (Rubio and Vigal, 1988), six from the Sierra de Alcaraz (Rubio et al., 2000), 10 in the Sierra Nevada (Meijide, 1987; Luzón-Ortega et al., 2002), and one from the Sierra del Aljibe (Donaire et al., 2001) (see Fig. 1).

2.3. Field work and identification of threats

Over a 16 year span (1990–2005), the authors and collaborators searched for the smooth snake *C. austriaca* in suitable areas of the Sierra Nevada. According to the historical *C. austriaca* records in this mountain (Meijide, 1987; Luzón-Ortega et al., 2002), we concentrated searches in alpine meadows between 2100 m and 2900 m altitude. Assuming low population densities, we repeatedly visited localities with old records in order to increase sampling success (Kéry, 2002). We searched on days with favourable climatic conditions (warm and sunny days), from approximately 9:00 h to 18:00 h. Sampling included searching for surface active snakes and turning over stones, because *C. austriaca* frequently warm up beneath rocks and other refugia exposed to the sun during daylight (Galán, 1998, 2004; Reading, 1997). Because *C. austriaca* relies heavily upon saurian prey (Galán, 1988), we also recorded the presence of *Podarcis hispanica* and *Psammodromus algirus* during sampling efforts in 2004 and 2005.

During the standardized sampling visits in 2004 and 2005, we identified and recorded potential human-related threats (i.e. habitat perturbations) to smooth snake *C. austriaca* populations in the southeastern mountains. This information, along with information on the ecological requirements revealed by our model is the basis we use to assess the conservation status of isolated populations of *C. austriaca* in southern Iberia.

2.4. Ecological model

We modelled the entire Iberian distribution of *C. austriaca* using a total of 1420 historic records from the Iberian Peninsula. These records were combined with ecogeographical GIS data to determine habitat suitability. Historic records were gathered from the atlases of amphibians and reptiles of Portugal (Godinho et al., 1999) and Spain (Pleguezuelos et al., 2002). These records were inscribed in a georeferenced database, assigned to the corresponding 10 × 10 km UTM quadrant, and displayed using ArcMap 9.0 GIS (ESRI, 2004). *C. austriaca* presence was recorded in a total of 531 quadrants (8.5% of the Iberian Peninsula area). The atlases of Portugal and Spain summarize considerable information collected by local experts during distinct herpetological studies, and haphazard encounters. More than 90% of records in these atlases are recent (from 1980 to present, Pleguezuelos et al., 2002), and thus, the information gathered in those atlases can be considered the present distribution of *C. austriaca*. Although no standardized sampling design was used to establish the herpetological distributions reported in these atlases, which cover the entire Iberian Peninsula (over 580,000 km^2 and more than 7500 UTM 10 × 10 km quadrants), the number of Iberian herpetologists surveyed in these compilations (more than 500; Godinho et al., 1999; Pleguezuelos et al., 2002), and the existence of local atlases for several counties suggest that the distributions of most species are well established. However, reliable distributional data for secretive and locally rare species like the smooth snake *C. austriaca* are likely not available in all the quadrants. Consequently, we used a modelling technique that uses only presence data: the Ecological Niche Factor Analysis (ENFA; Hirzel et al., 2002).

The distribution of *C. austriaca* in Iberia was modelled using 11 quantitative ecological and ecogeographical variables (hereafter EGV) selected for their general relevance to the snakes' ecology (Real et al., 1997; Brito and Crespo, 2002; Guisan and Hofer, 2003; Santos et al., 2006), including topographical, climatic, habitat, and biological variables (Table 1). Because interspecific competition can affect the distributions of snake species (Luiselli, 2006), we included the presence of potential ophidian competitors based on dietary affinities with *C. austriaca*. The size of grid cells (pixel) of most of the EGV was around 1 km^2 (see Table 1), whereas *C. austriaca* records were available at a 10 × 10 km resolution. To combine presence data and environmental data, EGV were resampled to a coarser resolution (10 × 10 km) using the "aggregate" function of ArcMap 9.0. Each output cell of the transformed EGV contained the mean value of the input cells encompassed by the output cell.

Ecological Niche Factor Analysis was developed using Biomapper 3.2 (Hirzel et al., 2007), following procedures outlined by Hirzel et al. (2002). In summary, ENFA compares the distribution of EGVs in the overall study area (i.e. the Iberian Peninsula) with their distribution within quadrants distinguished by smooth snake records. The EGVs were checked for variability and correlation. Two variables, ALTI and TEMP, were removed due to high correlations ($r > 0.800$) with TMIN. Marginality (the level at which the species niche differs from the available conditions in the study area) and Tolerance (the level at which the species lives in a narrow or wide range of conditions among those available in the study area) summarize in two single scores ranging from 0 to 1, the differences between EGVs in areas where the species is present, and in the overall study area (for additional details, see Hirzel et al., 2002). ENFA creates a habitat-suitability map by estimating the degree of similarity between each 10 × 10 UTM square and the ecogeographical preferences of the species. In other words, ENFA calculates the probability that a given square falls within the environmental domain of occupied areas. The habitat-suitability map derived from the geometric mean algorithm (Hirzel et al., 2002) yields values that vary from 0 (minimum habitat quality) to 100 (maximum). These scores were classified into three classes of suitability, based on Chefaoui et al. (2005): low habitat suitability (0–14); medium habitat suitability (15–44); and high habitat suitability (45–100). Squares with scores >45 have a high probability to harbour *C. austriaca*. In remaining squares, we predict that *C. austriaca* populations may survive only given the presence of adequate microhabitats, as mean environmental

Table 1 – Ecogeographical variables used in modelling the distribution of the smooth snake (*Coronella austriaca*) in the Iberian Peninsula.

Type	Code	Description, classes and units	Source	Original resolution
Topographical	ALTI	Altitude: 12 classes from 0 to 2822 m	USGS (2004)	30 arc second
	SLOP	Slope: 8 classes from 0% to 45%	Derived from USGS (2004)	"
Climatic	PDRY	Precipitation of the driest month: 10 classes from 0 to 99 mm	Hijmans et al. (2005)	"
	PWET	Precipitation of the wettest month: 10 classes from 32 to 271 mm	Hijmans et al. (2005)	"
	PSEA	Precipitation seasonality (coefficient of variation): 10 classes	Hijmans et al. (2005)	"
	TEMP	Average annual temperature: 10 classes from 3.0 to 18.6 °C	Hijmans et al. (2005)	"
	TMIN	Minimum temperature of the coldest month: 10 classes from −9.4 to 8.9 °C	Hijmans et al. (2005)	"
	TMAX	Maximum temperature of the warmest month: 10 classes from 12.4 to 36.5 °C	Hijmans et al. (2005)	"
	TSEA	Temperature seasonality (SD × 100): 10 classes	Hijmans et al. (2005)	"
Habitat	LCOV	8 Classes relating land cover (14 months data acquired by the VEGETATION sensor on-board SPOT 4 satellite between 1999 and 2000) with increasing levels of aridity: 1 – broad-leafed deciduous closed forest, 2 – needle-leafed evergreen forest, 3 – mixed leaf-type forest, 4 – deciduous shrub cover, 5 – closed-open herbaceous cover, 6 – sparse herbaceous-shrub cover, 7 – cultivated and managed areas, 8 – artificial surfaces and associated areas	GLC (2003)	740 × 740 m
Biological	COMP	4 Classes related to increasing number of competitor species: 1 – no competitors, 2 – presence of *Coronella girondica* or *Macroprotodon brevis* or *Malpolon monspessulanus*, 3 – presence of any two of these species, 4 – presence of all of these species	Godinho et al. (1999) and Pleguezuelos et al. (2002)	10 × 10 km

conditions for the species are not suitable at the geographical scale considered here (10 × 10 km squares). We assume that such populations are more vulnerable to local extinctions than are populations inhabiting quadrants of high habitat suitability. This information may be relevant for management planning of these very isolated populations at local and regional scales.

2.5. *Model validation*

The map generated by the model was evaluated for predictive accuracy by a cross-validation procedure, where species locations were randomly partitioned into k mutually exclusive sets, $k-1$ partitions were used to compute a habitat-suitability model, and the excluded partition was used to validate the model as independent data. This process was repeated k times, each time leaving out a different partition. Comparisons between k suitability maps followed the method described by Boyce et al. (2002), and further developed in Hirzel et al. (2006). Each map was reclassified into i bins, where each bin covered a proportion of the total study area (Ai) and contained some proportion of the validation points (Ni) (validation points were the observations excluded during cross-validation). The area-adjusted frequency of each bin was computed as $Fi = Ai/Ni$. The expected Fi for all bins was 1 when the model was completely random. For good models, low values of habitat suitability should have a low F scores (below 1) and high values should have high F scores (above 1) with a monotonic increase in between. The monotonicity of the curve was measured with a Spearman rank correlation of Fi, which is called the Boyce index B (Boyce et al., 2002). Validating models with the same data used in model construction may invalidate model extrapolation. However, comparative analysis of algorithm performance for model evaluation has demonstrated the ability of the Boyce index to provide insight into model quality and a reliable measure of presence-only based predictions (Hirzel et al., 2006).

3. Results

3.1. *Field work and threats to smooth snake C. austriaca populations*

Field searches for smooth snakes in the southern Iberian mountains yielded very poor success. We sampled potentially suitable areas of the Sierra Nevada for *C. austriaca* from 1990 to 2005, totalling 3583 h of field sampling, encountering only five snakes (one snake/717 h of field work). In the same area, we found 0.75 potential prey animals (lizards) per hour of fieldwork. All records of smooth snakes *C. austriaca* were from wet meadows located in high montane valleys (locally called "borreguiles", Fig. 2A), or from slopes immediately adjacent to borreguiles; all snakes were found under rocks. We also searched for *C. austriaca* in other southern mountain chains from which their presence has been recorded (see Fig. 1), however we did not find any new specimens. In the Sierra de Cazorla, we found southern smooth snakes, *Coronella girondica*, in an area where *C. austriaca* has previously been found (Rubio and Vigal, 1988). All new records were georeferenced, and incorporated in the database we used to build the predictive model.

The potential threats to the southeastern isolated populations of *C. austriaca* predicted from our field work, the analysis of local climatic data, and the register of recent human-

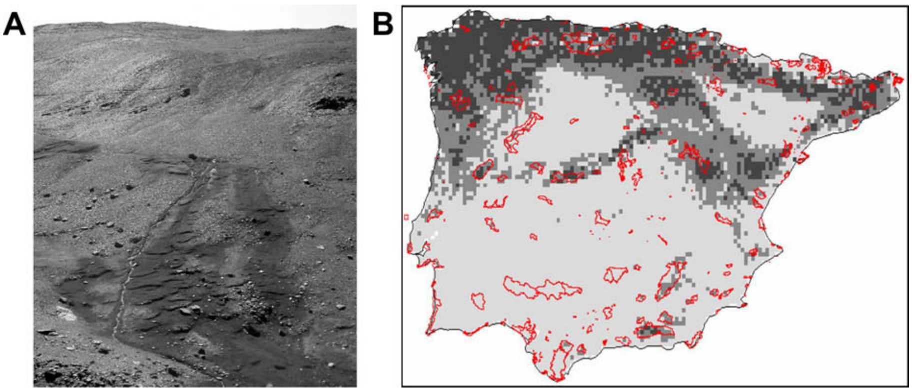

Fig. 2 – Map A: high elevation wet valleys in the Sierra Nevada, locally called "borreguiles", are suitable habitat for the smooth snake, *Coronella austriaca*. Map B: overlay of habitat suitability levels for the smooth snake *C. austriaca* with the Iberian protected areas. In the south, all highly suitable quadrants and some medium suitable 10 × 10 km quadrants are included in protected areas.

related perturbations, are: (1) habitat loss due to global warming and drought; in southeastern Iberia, temperatures have increased 0.07 °C each year over the last 22 years (Moreno-Rueda and Pleguezuelos, 2007), this increase in temperature has been accompanied by a 20% reduction in annual rainfall during the XX century (com. pers. A. Castillo). Both factors combine to reduce the surface of "borreguiles" in the Sierra Nevada. (2) Global warming may also facilitate increased interspecific competition with *C. girondica*, and predation by *Malpolon monspessulanus*, since the altitudinal limit of both species in the Sierra Nevada has increased in recent years (unpub. data of the authors). Furthermore, *M. monspessulanus* has increased in relative abundance, perhaps due to generalist habits and global warming (Segura et al., 2007; Moreno-Rueda and Pleguezuelos, 2007; Moreno-Rueda et al., in press). (3) Blanca et al. (2002) reported perturbations of Sierra Nevada "borreguiles" due to overgrazing that may degrade habitat quality for species such as the smooth snake. (4) In the Sierra Nevada, some historic localities are situated on Sol y Nieve ski station property. Ski slope maintenance during summers often includes rock disturbance and removal, vegetation removal and general alteration of smooth snake microhabitat. (5) Increasing populations of wild boar in the Sierra Nevada, as well as in other mountain ranges. Wild boar alter reptile habitat (Pleguezuelos, 2001; Galán, 2002), and within the study area, prey upon reptiles (unpub. data, authors). (6) Wildfires (Galán, 2002), that may impact *C. austriaca* localities in the Sierra de Segura and the Sierra de Cazorla.

3.2. *Habitat suitability*

The ecological model explained 87.7% of overall information and 75.4% of specialization. *C. austriaca* had a high marginality score (1.269) and a moderately high tolerance value (0.831). These results indicate that the species inhabits a moderately wide range of ecological conditions, although it occupies

Table 2 – Eigenvalues and percentage of specialization (the inverse of tolerance, i.e. the level at which the species live in a narrow or wide range of conditions among those available in the study area) explained by each factor of the ecological-Niche factor analysis and scores of the ecogeographical variables (EGV) that explain most of the variation in the occurrence of *Coronella austriaca* in the Iberian Peninsula (scores marked with * explain marginality and specialization). The first factor explains the marginality (the level at which the species niche differs from the available conditions in the study area) of the species and the remaining factors explain the specialization.

EGV	Factors								
	1	2	3	4	5	6	7	8	9
SLOP	0.370*	−0.010	0.063	0.040	−0.026	−0.245	−0.639	−0.058	0.167
PDRY	0.495*	−0.226	0.491	−0.314	0.079	0.087	−0.124	0.558	−0.767
PWET	0.297	0.506*	−0.029	0.149	−0.292	−0.372	0.481	−0.201	0.058
PSEA	−0.300	−0.520*	0.616	−0.043	0.334	−0.041	0.136	0.561	0.022
TMIN	−0.264	0.203	0.224	−0.493	0.308	−0.398	−0.141	−0.424	−0.414
TMAX	−0.482*	−0.003	−0.046	0.406	−0.690	0.430	−0.439	0.308	−0.435
TSEA	−0.221	−0.594*	0.507	−0.584	0.458	−0.416	0.302	−0.203	0.028
LCOV	−0.291	−0.010	−0.246	−0.141	−0.048	−0.520	−0.015	0.112	0.048
COMP	0.063	−0.166	0.069	−0.327	−0.114	0.083	0.149	−0.043	0.128
Eigenvalues	4.061	3.248	1.429	1.099	0.971	0.663	0.635	0.546	0.387
% Specialization	0.311	0.249	0.110	0.084	0.074	0.051	0.049	0.042	0.030

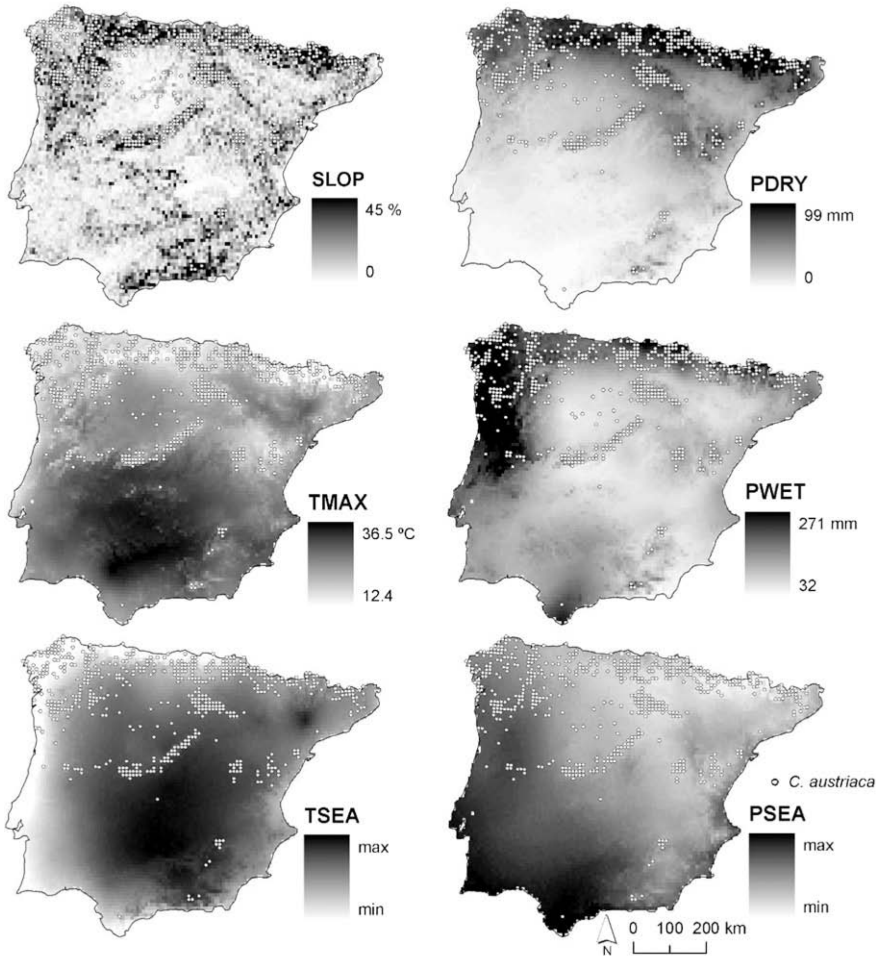

Fig. 3 – Distribution of *Coronella austriaca* in the Iberian Peninsula in relation to environmental factors explaining marginality (the level at which the species niche differs from the available conditions in the study area) and specialization (the inverse of tolerance) according to the ecological-Niche factor analysis: slope (SLOP), precipitation of driest month (PDRY), maximum temperature of warmest month (TMAX), precipitation of wettest month (PWET), temperature seasonality (TSEA), and precipitation seasonality (PSEA).

extreme habitat types with respect to the suite of habitats available in the Iberian Peninsula. *C. austriaca* presence was positively associated with slope and with precipitation during the driest month of the year, and was negatively associated with maximum temperatures during the warmest month (Table 2). Factors explaining specialization indicated that *C. austriaca* preferred rainy areas with reduced seasonality in temperature and precipitation (Fig. 3).

The habitat-suitability map categorized all UTM 10×10 squares of the Iberian Peninsula according to the existence of suitable *C. austriaca* habitat. Accuracy of model predictions was good, as area-adjusted frequency cross-validation (*Fi*) exhibited low variance, and values below and above 1 for the low and high suitability bins, respectively. The increase between these values was monotonic (mean Spearman rank correlation, $r = 1.0$, $P = 0.0$), and the Boyce index was 1.0 ± 0.0. The habitat-suitability map (Fig. 4) identified 1208 quadrants of high habitat suitability (296 with *C. austriaca* records, 24.5%), 1709 quadrants of medium habitat suitability (160 with *C. austriaca*, 9.4%) and 4646 quadrants of low habitat suitability (69 with *C. austriaca*, 1.5%). Highly suitable areas included the north and northwestern Atlantic coast, the Pyrenees, and isolated mountain chains in the Central and Iberian Systems. In contrast, the southeastern Iberian Peninsula contained just eight highly suitable quadrants, seven in the Sierra Nevada and a single quadrant in Sierra de Cazorla (Fig. 4). Although northern Iberia had numerous highly suitable quadrants located outside of protected areas, most highly suitable or medium suitable quadrants in the south were situated inside of, or close to, protected areas (Fig. 2B).

4. Discussion

Our models clearly indicate that populations of *C. austriaca* in southern Iberia are likely to be confined to small isolated patches of suitable habitat. The cool and rainy regions of the northern Iberian Peninsula, with less extreme seasonal changes in temperature and precipitation, represent the most suitable area for this snake (Fig. 3). The habitat-suitability map suggests that in the southern Iberian Peninsula, suitable

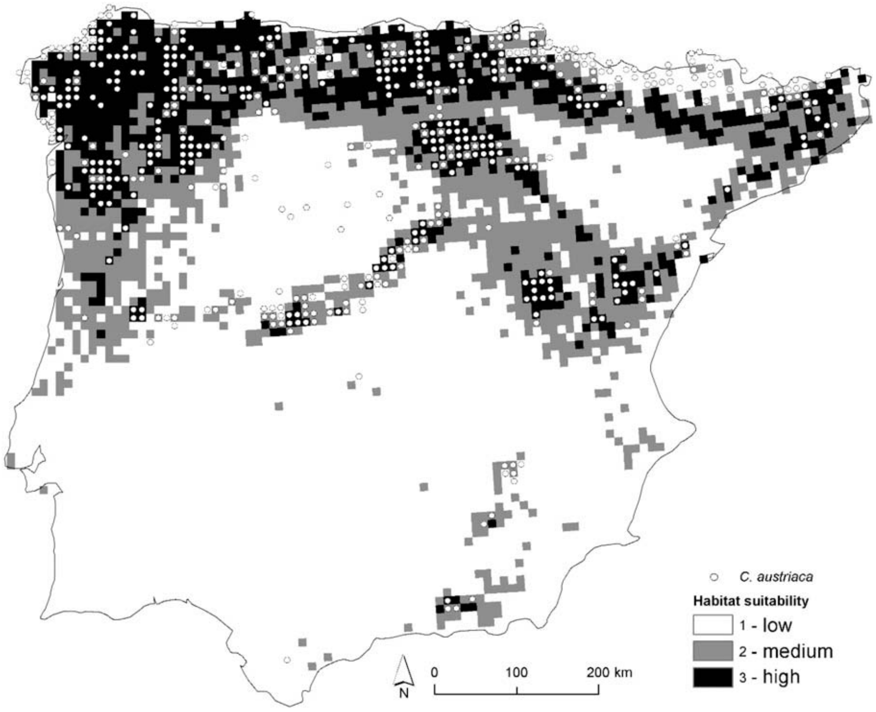

Fig. 4 – Habitat suitability for C. *austriaca* in the Iberian Peninsula. The map is derived from ecological-Niche factor analysis (see Section 2 for details) according to UTM 10 × 10 km grid size.

environmental conditions are restricted to a few mountain ranges (Fig. 4). The spatial resolution of analyses (10 × 10 km squares) is limited by available distribution information. However, in southern Iberia, a great variety of environments exist within each quadrant, due to the topographical complexity of these montane regions. Thus, we expect that analyses using finer grain size would identify highly suitable areas within 10 × 10 km quadrants. The extremely low number of C. *austriaca* records in southern Iberia makes this snake a good candidate for modelling on a finer scale. The existence of small populations in areas identified as suboptimal by our model (e.g. Sierra del Aljibe, Sierra de Alcaraz), suggest that these populations are highly vulnerable to local extinction. Accordingly, these populations are in need of areas of strict protection. The paucicity of historical records, supported by our field work, and results of our model, suggest that C. *austriaca* in the southern Iberian mountains are restricted to very small populations as a consequence of limited suitable habitat.

The main result of our model (low number of suitable areas in southern Spain) is supported by our field work. In southern Spain, high temperatures and low rainfall restrict suitable habitat for the smooth snake C. *austriaca* to a limited number of mountain ranges. Traditionally, these mountainous areas included relatively undisturbed natural habitats. However, our field work suggests that even in these undisturbed areas, the smooth snake C. *austriaca* seems to be restricted to small, fragmented sites where the snakes occur in low population densities. Furthermore, we recorded several anthropogenic threats in these sites that may increase vulnerability of the smooth snake populations to local extinction. The most important of these are habitat loss and disturbance. Climate change is expected to produce a global increase in temperature and local reductions in precipitation (IPCC, 2007). Both phenomena, already recorded in the south-eastern Iberian Peninsula, would act to reduce the number and extent of suitable C. *austriaca* localities, such as the wet “borreguiles” (Fig. 2A). In the same way, Araújo et al. (2006) predicted a loss of suitable areas for amphibian and reptile species mainly in southwest Europe, including the Iberian Peninsula. In addition, over the last decades, some high altitude sites have been affected by road construction, tourist infrastructure construction, and the recurrence of forest fires, serving to reduce suitable areas for C. *austriaca* and its prey (authors, pers. obs.). The combination of global and local threats argue for the establishment of long-term conservation measures, starting with the protection of areas containing suitable habitats in those localities not yet protected (see Fig. 2B). The extinction of C. *austriaca* in southern Iberian mountains should be viewed as entirely possible, as similar local extinctions have already occurred in the Sierra Nevada; several breeding Eurosiberian birds, including *Pyrrhocorax graculus* and *Turdus torquatus* have disappeared from the Sierra Nevada in recent years (Pleguezuelos, 1991; Pérez-Contreras and Rivas, 2001).

Life-history traits of the smooth snake C. *austriaca*, such as dietary specialization and low frequency reproduction may increase its vulnerability to local extinction in the southern Iberian mountains. In the Iberian Peninsula, C. *austriaca* is a lizard-eating specialist (82.1% of its diet in frequency, Galán, 1988); dietary specialization has been identified as a factor that increases extinction vulnerability in snakes (Dodd, 1993). In snakes, low food availability and viviparity can reduce reproductive output (Shine, 2003, 2005). These factors and the short activity period possible at high altitudes (e.g. in the Sierra Nevada snow covers potential habitat for five–six months per year), can difficult mature females to reproduce in consecutive years, hence limiting recruitment rates and restraining population growth.

Competition with *C. girondica* may also increase vulnerability of *C. austriaca* to local extinction. Both species are saurophagous, and syntopic in rainy areas of the northwestern Iberian Peninsula (Galán, pers. com.; Soares et al., 2005), although these species are not sympatric across most of southern Iberia, perhaps due to interspecific dietary competition (Capula et al., 1995). Our model suggested that climatic and topographical factors have a more profound relationship with *C. austriaca* occurrence than does the presence of competitor species. Nevertheless, recent observations from the Sierra de Cazorla and the Sierra Nevada (García-Cardenete and co-workers and Carretero and co-workers, pers. com.) demonstrate that *C. austriaca* and *C. girondica* do occur in sympatry in some southeastern Iberian mountains (at the upper altitudinal limit of *C. girondica* and the lower limit of *C. austriaca*). Global climate change could act to favour *C. girondica* in areas where it occurs in sympatry with *C. austriaca*; *C. girondica* is know to select dryer and sunnier areas than *C. austriaca* (Galán, 1988).

In summary, ecological modelling using large scale GIS was useful in assessing broad scale habitat suitability for Iberian populations of the smooth snake *C. austriaca*. At local scales, we identified several conservation threats that suggest vulnerability to local extinction. Molecular studies have shown that southern Iberian *C. austriaca* populations are genetically well differentiated (Santos et al., 2008). Accordingly, extinction of these populations is a conservation concern, and would reduce biodiversity of the Iberian Peninsula, one of the regions with the greatest biodiversity of amphibians and reptiles in Europe (Gasc et al., 1997). We suggest that the complete protection of all the southern Iberian localities with suitable smooth snake habitat is essential. We also suggest that efforts to increase the current knowledge of smooth snake *C. austriaca* demography, activity and life-history traits are urgently needed.

Acknowledgments

We thank V. Albin, A. González, M. Sicilia and A. Tinaut for helping in field work, the Asociación Herpetológica Española for providing the database used in analyses, and the anonymous reviewers who improved the quality of the final work. K. Setser improved the style of the manuscript. X. Santos is supported by a Beatriu de Pinós postdoctoral Grant from the Generalitat de Catalunya (BP-B1 10211), J.C. Brito (SFRH/BPD/26699/2006) and N. Sillero (SFRH/BPD/26666/2006) are supported by post-doctoral Grants from Fundação para a Ciência e Tecnologia (FCT, Portugal). This study was partially funded by the Consejería de Medio Ambiente (Junta de Andalucía) through a project coordinated by J.M. Pleguezuelos. Permits for field searching in Sierra Nevada were provided by the central bureau of the National Park.

REFERENCES

Araújo, M.B., Thuiller, W., Pearson, R.G., 2006. Climate warning and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33, 1712–1718.

Blanca, G., López Onieva, M.R., Lorite, J., Martínez-Lirola, M.J., Molero-Mesa, J., Quintas, S., Ruiz-Girela, M., Varo, M.A., Vidal, S., 2002. Flora amenazada y endémica de Sierra Nevada. Universidad de Granada, Universidad de Granada-Consejería de Medio Ambiente, Junta de Andalucía, Granada.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecological Modelling 157, 281–300.

Brito, J.C., Crespo, E.G., 2002. Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the Northwestern Iberian Peninsula. In: Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H.W. (Eds.), Biology of the Vipers. Eagle Mountain Publishing, pp. 129–138.

Capula, M., Luiselli, L., Rugiero, L., 1995. Ecological correlates of reproductive mode in reproductively bimodal snakes of the genus *Coronella*. Viet et Milieu 45, 167–175.

Chefaoui, R.M., Hortal, J., Lobo, J.M., 2005. Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian *Copris* species. Biological Conservation 122, 327–338.

Coope, G.R., 1994. The response of insect fauna to glacial–interglacial climatic fluctuations. Philosophical Transactions of the Royal Society of London, Series B 344, 19–26.

Dodd Jr., C.K., 1993. Strategies for snake conservation. In: Seigel, R.A., Collins, J.T. (Eds.), Snakes – Ecology and Behavior. McGraw Hill, New York, pp. 363–394.

Donaire, D., Cuadrado, A., González, J.P., Barnestein, J.A.M., 2001. Sobre la presencia de *Coronella austriaca* (Laurenti, 1768) en la mitad sur de la Península Ibérica. Butlletí de la Societat Catalana d'Herpetologia 15, 115–120.

Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology 41, 263–274.

ESRI, 2004. ArcMap 9.0. Environmental Systems Research Institute, Inc.

Frankham, R., Ballou, J.D., Briscoe, D.A., 2004. A Primer of Conservation Genetics. Cambridge University Press, Cambridge.

Galán, P., 1988. Segregación ecológica en una comunidad de ofidios. Doñana, Acta Vertebrata 15, 59–78.

Galán, P., 1998. *Coronella austriaca* Laurenti, 1768. In: Salvador, A. (Coord.), Ramos, M.A. et al. (Eds.), Fauna Ibérica: Reptiles, vol. 13, Museo Nacional de Ciencias Naturales, CSIC, Madrid, pp. 364–375.

Galán, P., 2002. *Coronella austriaca* (Laurenti, 1768). Culebra lisa europea. In: Pleguezuelos, J.M., Márquez, R., Lizana, M. (Eds.), Atlas y libro rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza and Asociación Herpetológica Española, Madrid, pp. 277–279.

Galán, P., 2004. Culebra lisa europea – *Coronella austriaca*. In: Carrascal, L.M., Salvador, A. (Eds.), Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid (<http://www.vertebradosibericos.org/>).

Galán, P., Fernández-Arias, G., 1993. Anfibios é reptiles de Galicia. Edicions Xerais de Galicia, Vigo, Spain.

Gasc, J.-P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez-Rica, J.P., Maurin, H., Oliveira, M.E., Sofianidou, T.S., Veith, M., Zuiderwijk, A., 1997. Atlas of Amphibians and Reptiles in Europe. Societas Europaea Herpetologica and Muséum National d'Histoire Naturelle (IEGB/SPN), Paris.

GLC, 2003. The Global Land Cover for the Year 2000. <http://www-gvm.jrc.it/glc2000/defaultGLC2000.htm>.

Godinho, M.R., Teixeira, J., Rebelo, R., Segurado, P., Loureiro, A., Álvares, F., Gomes, N., Cardoso, P., Camilo-Alves, C., Brito, J.C., 1999. Atlas of the continental Portuguese herpetofauna: an assemblage of published and new data. Revista Española de Herpetologia 13, 61–82.

Guisan, A., Hofer, U., 2003. Predicting reptile distributions at mesoscale: relation to climate and topography. Journal of Biogeography 30, 1233–1243.

Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A., Zimmermann, N.E., 2006. Using Niche-based models to improve the sampling of rare species. Conservation Biology 20, 501–511.

Hewitt, G.M., 2000. The genetic legacy of the quaternary ice ages. Nature 405, 907–913.

Hewitt, G.M., 2003. Ice ages: their impact on species distributions and evolution. In: Rothschild, L.J., Lister, A.M. (Eds.), Evolution on Planet Earth. Academic Press, New York, pp. 339–361.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978 (<http://www.worldclim.org/>).

Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-Niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83, 2027–2036.

Hirzel, A.H., Hausser, J., Perrin, N., 2007. Biomapper 3.2. Laboratory for Conservation Biology, Department of Ecology and Evolution, University of Lausanne, Switzerland. <http://www2.unil.ch/biomapper>.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199, 142–152.

IPCC, 2007. Climate Change 2007. Synthesis Report, Intergovernmental Panel on Climate Change, Valencia, Spain.

Kéry, M., 2002. Inferring the absence of a species – a case study of snakes. Journal of Wildlife Management 66, 330–338.

Lesica, P., Allendorf, F.W., 1995. When are peripheral populations valuable for conservation? Conservation Biology 9, 753–760.

Luiselli, L., 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114, 193–211.

Luzón-Ortega, J.M., García-Cardenete, L., Pérez-Contreras, J., Fernández-Cardenete, J.R., 2002. Culebra lisa europea (*Coronella austriaca*), nuevas citas y récord altitudinal para Europa Occidental en Sierra Nevada (SE Iberico, España). Acta Granatense 1, 148–150.

Meijide, M., 1987. Hallazgo de *Coronella austriaca* en Sierra Nevada, Granada (España). Revista Española de Herpetología 2, 187–188.

Moreno-Rueda, G., Pleguezuelos, J.M., 2007. Long-term and short-term effects of temperature on snake detectability in the wild: a case study with *Malpolon monspessulanus*. Herpetological Journal 17, 204–207.

Moreno-Rueda G., Pleguezuelos J.M., Alaminos E., in press. Climate warming and activity period extension in reptiles: evidence from the Mediterranean snake *Malpolon monspessulanus*. Climatic Change. doi:10.1007/510584-008-9469-y.

Pérez-Contreras, J., Rivas, J.M., 2001. Avifauna. In: V. García-Canseco (Coord.), Parque Nacional de Sierra Nevada. Canseco Editores, Talavera de la Reina, pp. 185–208.

Pleguezuelos, J.M., 1991. Evolución histórica de la avifauna nidificante en el SE de la Península Ibérica (1850–1985). Consejería de Cultura y Medio Ambiente, Junta de Andalucía, Sevilla.

Pleguezuelos, J.M., 2001. Introducción al estado de conservación de los reptiles en Andalucía. In: Franco, A., Rodríguez de los Santos, M. (Eds.), Libro Rojo de los Vertebrados de Andalucía. CMA, Sevilla, pp. 49–58.

Pleguezuelos, J.M., Márquez, R., Lizana, M. (Eds.), 2002. Atlas y Libro Rojo de los Anfibios y Reptiles de España. Dirección General de Conservación de la Naturaleza and Asociación Herpetológica Española, Madrid.

Pough, F.H., 1980. The advantages of ectothermy for tetrapods. The American Naturalist 115, 92–112.

Real, R., Pleguezuelos, J.M., Fahd, S., 1997. The distribution patterns of reptiles in the Rif region, northern Morocco. African Journal of Ecology 35, 312–325.

Reading, C.J., 1997. A proposed standard method for surveying reptiles on dry lowland heath. Journal of Applied Ecology 34, 1057–1069.

Rubio, J.L., Benayas, J., Blanco, R., 2000. *Coronella austriaca* (Culebra lisa europea), nueva cita en la Sierra de Alcaraz (Albacete). Boletín de la Asociación Herpetologica Española 11, 19–20.

Rubio, J.L., Vigal, C.R., 1988. Primeras citas de *Coronella austriaca* en Jaén y Albacete. Revista Española de Herpetología 3, 143–144.

Santos, X., Brito, J.C., Sillero, N., Pleguezuelos, J.M., Llorente, G.A., Fahd, S., Parellada, X., 2006. Inferring habitat-suitability areas with ecological modelling techniques and GIS: a contribution to assess the conservation status of *Vipera latastei*. Biological Conservation 130, 416–425.

Santos, X., Roca, J., Pleguezuelos, J.M., Donaire, D., Carranza, S., 2008. Biogeography and evolution of the Smooth snake *Coronella austriaca* (Serpentes: Colubridae) in the Iberian Peninsula: evidence for Messinian refuges and Pleistocenic range expansions. Amphibia–Reptilia 29, 35–47.

Segura, C., Feriche, M., Pleguezuelos, J.M., Santos, X., 2007. Specialist and generalist species in habitat use: implications for conservation assessment in snakes. Journal of Natural History 41, 2765–2774.

Shine, R., 2003. Reproductive strategies in snakes. Proceedings of the Royal Society of London, Series B 270, 995–1004.

Shine, R., 2005. Life-history evolution in reptiles. Annual Review of Ecology, Evolution, and Systematics 36, 23–46.

Soares, C., Álvares, F., Loureiro, A., Sillero, N., Arntzen, J.W., Brito, J.C., 2005. Atlas of the amphibians and reptiles of Peneda-Gerês National Park, Portugal. Herpetozoa 18, 155–170.

Soulé, M.E., Khom, K.A., 1989. Research Priorities for Conservation Biology. Island Press, Washington, DC.

Strijbosch, H., 1997. *Coronella austriaca* Laurenti, 1768. In: Gasc, J.-P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbachner, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H., Oliveira, M.E., Sofiandou, T.S., Veith, M., Zuiderwijk, A. (Eds.), Atlas of Amphibians and Reptiles in Europe. Societas Europea Herpetologica and Muséum National d'Histoire Naturelle (IEGB/SPN), Paris, pp. 344–345.

Ursenbacher, S., Conelli, A., Golay, P., Monney, J.-C., Zuffi, M.A.L., Thiery, G., Durand, T., Fumaggali, L., 2005. Phylogeography of the asp viper (*Vipera aspis*) inferred from mitochondrial DNA sequence data: evidence for multiple Mediterranean refugial areas. Molecular Phylogenetics and Evolution 38, 546–552.

USGS, 2004. Shuttle Radar Topography Mission (SRTM): Mapping the World in 3 Dimensions. <http://www.srtm.usgs.gov/index.html>.