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

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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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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
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. Soule 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...
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; Lu-zón-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; Lu-zón-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 hazard 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 km² 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 quantitatively ecological and ecogeographical variables (hereafter EGV) selected for their general relevance to the snakes’ ecology (Rea 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 km² (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

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; Luzzi-on-Ortega et al., 2002), and one from the Sierra del Aljibe (Donaire et al., 2001) (see Fig. 1).
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 gironica, 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-
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

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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
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 paucity 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 southeastern 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, 2006).
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. g. may also increase vulnerability of C. a. 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. a. 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. a. and C. g. do occur in sympathy in some southeastern Iberian mountains (at the upper altitudinal limit of C. g. and the lower limit of C. a.). Global climate change could act to favour C. g. in areas where it occurs in sympathy with C. a.; C. g. is known to select dryer and sunnier areas than C. a. (Galán, 1998).

In summary, ecological modelling using large scale GIS was useful in assessing broad scale habitat suitability for Iberian populations of the smooth snake C. a. At local scales, we identified several conservation threats that suggest vulnerability to local extinction. Molecular studies have shown that southern Iberian C. a. 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 knowl-

**Acknowledgments**

We thank V. Albin, A. González, M. Sicilia and A. Tintau 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. Plegueuelas. Permits for field searching in Sierra Nevada were provided by the central bureau of the National Park.

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