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MODELLING AND MAPPING SNAKE DISTRIBUTIONS IN SPAIN UNDER A
CLIMATE CHANGE SCENARIO

by

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the Faculty of Graduate Studies and Research
in partial fulfilment of the requirements for the degree of

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ABSTRACT

Logistic regression was explored to simulate the potential impact of climate change on the distribution of the thirteen snake species present in the Spanish Iberian Peninsula. The results obtained allowed classification of the Spanish snakes into: species widely distributed, not amenable to be modelled; species widely distributed in the Mediterranean region, not amenable to be modelled; Eurosiberian species limited by precipitation; and Mediterranean species limited by temperature. The implementation of the climate change scenario into the logistic models illustrated the magnitude of effects that might be expected as a consequence of global climate change: *Coronella austriaca*, *Coluber viridiflavus* and *Elaphe longissima* face entirely or almost entirely unsuitable conditions for persistence. *Hemorrhois hippocrepis*, *Macroprotodon brevis* and *Vipera seoanei*, might experience drastic extirpations and fragmentations of their current distributional areas and might extend their distributions to new areas. Finally, *Vipera aspis* might be particularly favoured by the projected effects of global warming.

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CHAPTER 1

INTRODUCTION

Habitat modelling and the prediction of the geographic distribution of species are growing fields of study in biogeography (e.g. Mladenoff et al., 1996; Li et al., 1997; Stockwell and Peterson, 1999). A major application area is the prediction of changes of species distribution based on alterations to current habitats produced by land use change or climate change.

Climate is characterized as a synthesis of the atmospheric conditions over time, that is, the physical state of the atmosphere at a particular site during a particular time period. Over Earth's long history, climate has undergone many changes due to natural dynamic processes. There have been warm periods and cold periods; but recent records indicate a warming tendency over the last century (IPCC, 2001). Leaving aside whether this change is a human or natural induced issue, it is widely agreed that climate warming is currently occurring. According to the Intergovernmental Panel on Climate Change (IPCC), global mean temperature has increased by 0.6°C over the last century (IPCC, 2001). In addition, during the 20th century, precipitation has increased between 5 and 10 % in middle and high latitudes of the Northern hemisphere and has decreased by 3 % in most of the subtropical terrestrial areas (IPCC, 2001). As a result, most climate change scenarios predict increases in the global mean precipitation although particular regions will become drier (IPCC, 2001).

With climate warming having been determined as the current trend of Earth, it is essential to understand its effects on all organization levels. It is also important to predict

the upcoming biological effects of climate change in response to projected future climate change scenarios.

Alterations in precipitation and temperature as well as CO₂ concentrations are acting as “vectors of change” (Lorente et al., 2004) for the biological systems. The projected ecological consequences of these “vectors of change” undoubtedly will show differences when addressed at different temporal and spatial scales and in different species. Even though genetic changes can occur relatively quickly in some cases (Rodríguez-Trelles and Rodríguez, 1998), migration and extirpation, if not extinction, are expected to be the main response of plants and animals to climate warming (Huntley, 1995). Numerous organisms appear to be limited by temperature, at least in parts of their geographic range (Brown and Lomolino, 1998). In these terms, many species that are affected by warmer than desirable conditions have been observed to change their ranges polewards in latitude and/or upwards in elevation (Parmesan, 1996).

Other effects of climate change that have been detected are related to the physiology and phenology of some organisms. For example, some species of plants have shown a delay in the change of leaf colour (Menzel and Fabian, 1999) and earlier flowering (Fitter and Fitter, 2002). There are also examples of earlier bird egg laying (Crick and Sparks, 1999), insect flight (Parmesan et al., 1999), and amphibian breeding (Beebee, 1995).

This study will be based on the niche theory and will be focussed at the population level, looking at the distributional changes that selected species of snakes will be expected to experience under future climate change scenarios. While natural history evidence indicates that there have been past changes in the distribution ranges of reptiles,

these changes have occurred over longer time scales than is suggested by the currently projected situation of climate change. Therefore, migrations, extirpations and extinctions could be expected for these taxa.

Herpetofauna are believed to be particularly vulnerable to climate change (Janzen, 1994; Pounds et al., 1999; Gibbons et al., 2000; Hughes, 2000; Kiesecker, 2001). From a physiological perspective, temperature and moisture are the two most important components of climate that impact directly on snakes. In addition, because of their restricted dispersal skills, they are especially vulnerable to rapid habitat changes and may experience proportionally more extirpations and extinctions, as a result of a rapid change of climate than, for example, birds (Gibbons et al., 2000).

The decrease of biodiversity has attracted much attention during recent years, yet discussions of biodiversity in mainstream conservation literature infrequently mention snakes. Consistent methods of status determination and the development of management strategies for snake populations have, in general, not been developed. Research should be directed at questions relating to deficiencies in knowledge of snake biology and distribution. Furthermore, very little research has been conducted on population viability analysis of snake species (Dodd, 1993). The current research was developed as an attempt to make some progress towards improving knowledge levels about snakes and their response to environmental change.

In the Western Palearctic region, the Iberian Peninsula represents an area of special interest for biodiversity because it is the richest and most biologically diverse region in Western Europe (Ramos et al., 2001). Three main reasons allow Spain, which occupies most of the Iberian Peninsula, to hold this biodiversity: its geographical

situation that leads to the existence of different climates, its mountainous relief, and its land use history that has allowed the retention of huge areas of natural landscapes.

Spain is the second most mountainous country in Europe. Its average altitude is 660 m above sea level with large mountains chains mainly running East-West. This particular orographic aspect, together with the influences of the Atlantic Ocean, the Mediterranean Sea and the Sahara Desert make the Iberian Peninsula able to harbour a wide range of climates. Thus, it has extremely wide ranges of precipitation, temperature, solar radiation and regional winds. While mean annual temperature in most of Spain ranges between 14 and 20 °C, the combination of altitude and continentality leads many areas to reach extremes of 30°C in a single day and ranges of more than 60°C over the year (MMA, 2000).

The Iberian Peninsula is part of the Holarctic flora and fauna and forms part of two biogeographic regions (Figure 1.1): Eurosiberian and Mediterranean. The amount of precipitation provides the clearest separation between these regions.

The “Brown Spain” or Mediterranean region has abundant sunshine throughout the year; mild winters on the coast and severe winters inland; and extremely irregular rainfall in spring, autumn, and winter. Summers are hot and usually characterized by a drought of varying length. On the other hand, the “Green Spain” has a similar climate to Western Europe, with mild winters, cool summers, moist air, frequent cloudy periods and frequent rainfall during the year (MMA, 2000).

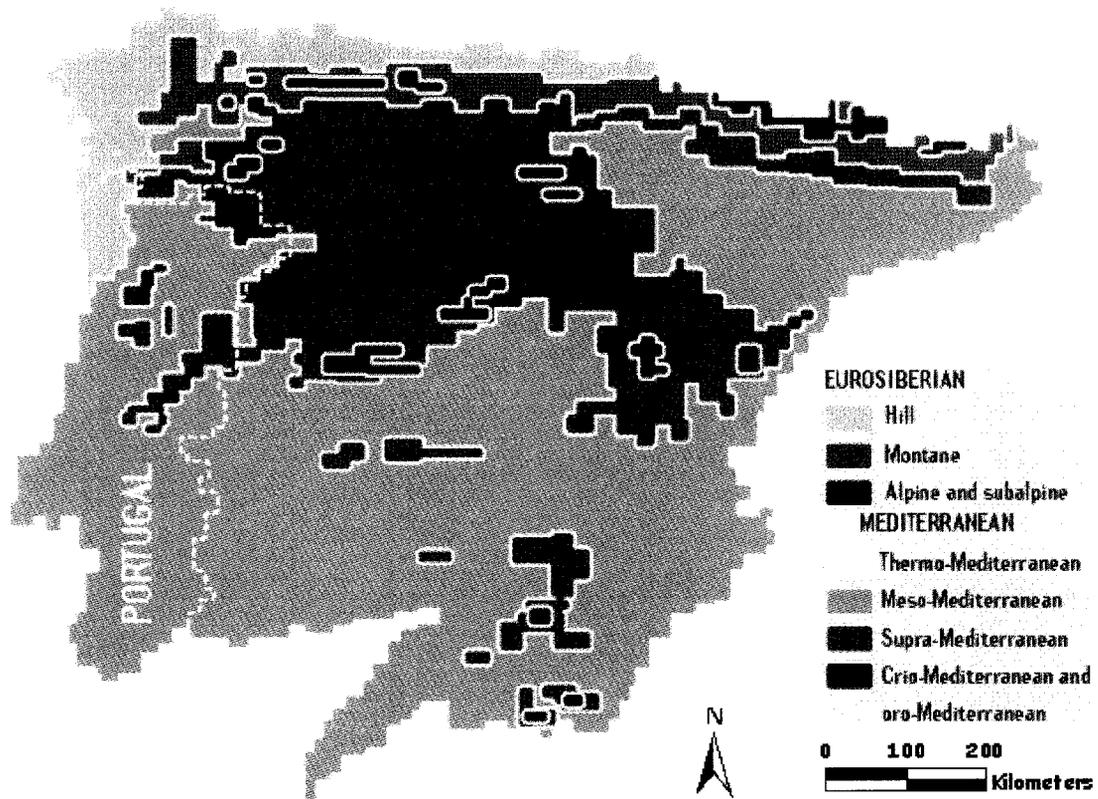


Figure 1.1: Biogeographic regions and bioclimatic storeys of the Iberian Peninsula. Adapted from MMA (2000).

1.1 Research question

The central purpose of this study is to explore a methodology for the prediction of the distribution of specific snakes species in the Spanish Iberian Peninsula under a future climate change scenario. For this purpose, a series of logistic regression models for selected species will be developed using geographic locations, recent climatic variables and current snake distribution datasets. The future distribution of each species will be projected by substituting the future projections of climate variables in these logistic regression models.

1.2 Thesis organization

This thesis has been organized into five chapters. Chapter two describes the most relevant areas upon which this study is based. The data and methodology used are described in chapter three while chapter four presents and discuss the results. Finally, chapter five provide concluding remarks about the major research findings, limitations and future research directions.

CHAPTER 2 BACKGROUND

The main fields on which this study is based are reviewed in this section. The first part focuses on the biology of snakes, emphasizing those characteristics that are more relevant when a likely climate warming is considered. Subsequently, the various hypotheses elaborated by biogeographers during the last century about the relation between climate and species distributions are described. Finally, some of the techniques developed in recent years to predict species distributions and their limitations are explained, giving special attention to logistic regression analysis.

2.1 Biology of snakes

Two major biological issues of snakes are pertinent to this study: first, the nature of their dependence on temperature and water, because these variables are very susceptible to change under future global warming; second, their ability to adapt by migrating to suitable habitats, if their current location becomes inappropriate for living.

Lizards and snakes together compose the order Squamata, within which snakes are classified in the suborder Serpentes (Pough et al., 2001). Some characteristics of this suborder are that they are limbless or have reduced limbs and they have an elongated flexible body with no sharp differentiation of neck, thorax and abdomen. No snake has any trace of forelimbs, shoulder girdle or breast bone; and in the majority, there are no vestiges of hind limbs or pelvis (Parker and Grandison, 1977). This corporal structure allows the development of the characteristic horizontal “serpentine” locomotion common to all snakes (Bellairs and Attridge, 1975).

The suborder Serpentes comprises approximately 15 families and more than 2,500 species of snake. The snakes of Spain belong to two families: Viperidae and Colubridae. Most Viperidae are stout-bodied with a short tail, flat and triangular head, and vertical eye pupil (Steward, 1971). Furthermore, they have a powerful venom which is injected by their long tubular fangs.

The family Colubridae encompasses about 70 % of Serpentes species and exhibits a considerable range of diversity, adaptation and specialization. None has a pelvis or hind limbs and the left lung is reduced or absent (Parker and Grandison, 1977). They have large scales, usually nine, covering the top of the head and they lack perforated venom fangs at the front of their mouth although some species may have a few fangs in the rear of their upper jaw (Steward, 1971).

2.1.1 Biophysical ecology

Biophysical ecology is the study of the way animals exchange heat and water with their environment (Pough et al., 2001). Homeothermic endothermic animals control the temperature of the body at an almost constant level; ectothermic animals whether heterothermic or homeothermic lack the ability to control their body temperature. When the ambient temperature falls below the control level, endothermic animals minimize the heat loss by having insulating layers of hair, feathers or fat and the heat lost is metabolically compensated. Conversely, when the external temperature is high, their body temperature is prevented from rising by an increase in the rate of water evaporation from their body surfaces and the panting rate is increased (Parker and Grandison, 1977).

Ectothermic animals, like snakes, do not have heat-insulating layers or the adaptations that allow temperature regulation at a constant level. Under cool conditions, heat losses are often too great to be compensated by metabolic heat, at least under resting conditions. Also, when the environmental temperature increases snakes are equally incapable of controlling their body temperature physiologically because they do not have sweat glands and their panting control is limited.

Snakes must maintain their body temperature within the temperature range of about 4-38°C. When the temperature decreases below 2-4°C, they become totally torpid and when it rises to 38-47°C, they can die because some of their tissue proteins suffer permanent chemical changes. The optimal temperature range is more narrowly bounded; the average limits for most species lie between 21-37°C (Parker and Grandison, 1977).

In the absence of structural and physiological regulators, body temperature control is achieved by behaviour. Habits of snakes differ considerably according to climatic conditions. For example, if temperature is low, they will tend to stay in open spaces basking in the sun; if temperature is high, they will tend to look for shade and refuge. Furthermore, ambient temperature variation may influence snake population dynamics by affecting growth, reproductive output, and survivorship (Parker and Grandison, 1977).

Snakes living in cooler environments tend to grow more slowly during the course of the year, reproduce less frequently, and live longer (Brown, 1991). On the other hand, in climates where the air temperature remains constantly above the minimum temperature at which they are active, including some areas in the south of Spain, there is no period of winter hibernation and the principal danger is the midday sun. Under these conditions, species with nocturnal or crepuscular habits have an advantage and diurnal species tend

to operate in the shade or become crepuscular, remaining under cover during the heat of the day. They aestivate at the peak of the hot season, remaining inactive for long periods. This mechanism of remaining motionless is totally controlled. On the other hand, in high latitudes or altitudes, survival through winter is only possible if a frost-free underground refuge for hibernation can be found. This is the factor that determines the geographical and topographical limits of snakes. None can survive where the subsoil remains frozen throughout the year, as it does in some Spanish mountains. During hibernation, they are in a state of physiological torpor directly produced by a low ambient temperature. When the midday temperature begins to fall, a migration towards the underground refuge may start. As the cold season advances, their visits to the surface become progressively shorter and finally cease until temperature rises sufficiently. The duration of this inactive period ranges from a few days to eight months per year according to topographical and geographical climatic differences (Parker and Grandison, 1977). In the coldest climates, growth is slow, and the reproductive cycle is prolonged so that young are produced every two years instead of annually. Furthermore, as the number of nights on which the temperature remains above 21 °C decreases, nocturnal species become more disadvantaged until they can no longer survive unless they change their habits (Parker and Grandison, 1977). Thus, species can be nocturnal or crepuscular in the south of their range but more diurnal in the north. In spring and autumn, snakes can raise their body temperature above the air temperature by basking in the sun. The rate at which this rise takes place depends on the solar radiation intensity and on the animal's size and colour. Smaller forms have less mass to heat; this allows them to have longer periods of activity in cool but sunny weather. Consequently, the snakes of the colder regions are generally

smaller. It is also frequently found that where a species has a wide altitudinal range, there are dwarf races at higher altitudes, which may also be darker in colour to absorb more sun rays (Parker and Grandison, 1977).

With regards to their relationship to water, reptiles were the first vertebrates to have become completely terrestrial. However, some reptiles cannot exist without free water, and free water is indispensable for the development of the eggs of some species of snakes (Cloudsley-Thompson, 1971). Respiration in snakes takes place mainly through their lungs, and although the reptilian skin shows low permeability for water, ions and gases, there are numerous exceptions and great interspecific variability. Reptiles regulate their water and electrolyte fluxes both physiologically and behaviourally. For example, several desert snakes make wiping movements with their heads along their bodies during which they probably spread lipid secretions that reduce evaporative water loss. Along similar lines, the Montpellier snake (*Malpolon monspessulanus*), a species widely distributed in Spain, has been shown to possess nasal glands that secrete fluids containing long chain fatty acids. Furthermore, many reptiles are opportunistic drinkers, selective in their food intake, and as already discussed, hibernate or aestivate when conditions become unfavourable (Cloudsley-Thompson, 1999).

2.1.2 Diet

There are no vegetarians and very few carrion feeders amongst snakes. Although many of the larger snakes may have a varied diet, their food intake can change with age as their increasing size enables them to eat larger prey. The majority have limited food preferences; some feed exclusively on frogs, others on lizards or on rodents, while a large

number have a diet consisting almost exclusively of other snakes. In a few instances, the preferred food may consist of only a single abundant species, but such narrow specialization is unusual (Parker and Grandison, 1977).

2.1.3 Reproduction

Most snakes are oviparous, that is they lay eggs, but many give birth to live young (Ovoviviparous). What usually happens in the latter case is that the eggs are simply retained inside the body of the mother snake until the young are hatched (Logier, 1958).

The usual pattern in temperate zones is for ova to develop to maturity during the winter months and for mating to occur in spring as soon as hibernation ends (Parker and Grandison, 1977). Nevertheless, environmental conditions may prevent snakes from obtaining sufficient energy so that females reproduce on a multiyear rather than an annual cycle (Peterson et al., 1993). This situation could occur in regions with short summers.

2.1.4 Mobility

Reptiles move from one place to another for many reasons, but ultimately all movements are related to the acquisition of resources. Variation in home range size is related to the spatial and temporal distribution of resources, particularly food (Pough, 1998). It is expected that global warming will alter the patterns of resource distribution. Therefore, reptiles will have to be able to face these changes by means of adaptation or migration.

Most herpetofauna confine their routine activities to a limited home range. However, the sizes of home ranges vary significantly among species. As shown in Table

2.1, reptiles have larger home ranges than amphibians. This has direct consequences for the current research in which the standard cell size used was 100 km² (10 x 10 km). Microhabitats within the cells and other very local factors will not be described by the logistic models, which will affect the ability to model effects of climate change for species whose individual home ranges are smaller than this size. Alternatively, species whose individual home ranges are larger will be determined by macroecological factors such as climate or topography. As shown on Table 2.1, snakes were selected in this study because, within herpetiles, they are the ones that cover the largest areas.

Table 2.1: Approximate home range sizes of selected herpetofaunal groups (Adapted from Pough et al., 1998)

	Group	Range (m ²)
Reptiles	Colubridae (snakes)	9-210,000
	Viperidae (snakes)	800-60,000
	Lizards (males)	10-20,000
	Lizards (females)	15-1,000
Amphibians	Anurans	1-1,900
	Caudates	0,1-87

Migration abilities are another movement issue that needs to be considered. As explained above, reptiles appear to be limited by temperature. Because a 3°C change in mean annual temperature corresponds to a shift in isotherms of 300–400 km in latitude or 500 m in altitude (Hughes, 2000), drastic changes in species distributions are expected in response to climatic shifts. Hence, if snakes are not able to adapt to the local climate, they will have to migrate to suitable habitats. Because of their low dispersal rates (Brito, 2003), combined with habitat loss, it is very likely that climate change will produce high rates for snakes. Pleguezuelos (pers. comm.) estimates that given suitable conditions, a small species like *Vipera seoanei* would be able to migrate around 1 km per year to face

climate change; larger species of colubrids would be able to migrate more rapidly. Therefore, in this study, *Vipera seoanei* could potentially disperse around two cells (20 km) away from their current distribution by 2020. Based on this rule of thumb and the size of the animals, I have estimated the number of cells that each species of Spanish snakes would be able to move from their current distribution by 2020 (Table 2.2)

Table 2.2: Hypothesized number of cells that the Spanish snakes would be able to cover from their current distribution to 2020.

Species	Body size (mm)	Number of cells covered by 2020
<i>Coronella austriaca</i>	700	3.1
<i>Coronella girondica</i>	600	2.6
<i>Hemorrhois hippocrepis</i>	1500	6.6
<i>Coluber viridiflavus</i>	1200	5.3
<i>Elaphe longissima</i>	1100	4.8
<i>Elaphe scalaris</i>	1100	4.8
<i>Macropododon brevis</i>	450	2
<i>Malpolon monspessulanus</i>	1800	8
<i>Natrix maura</i>	750	3.3
<i>Natrix natrix</i>	800	3.5
<i>Vipera aspis</i>	600	2.6
<i>Vipera latastei</i>	550	2.4
<i>Vipera seoanei</i>	450	2

2.1.5 Proposed model of habitat selection

Reinert (1993), based on studies of bird habitat selection, proposed a model for snakes illustrated in Figure 2.1. This model recognizes two components of habitat selection: macrohabitat and microhabitat. It suggests that there is a hierarchical response to these two scales of spatial heterogeneity. Under this model, physiological factors are seen as the major initiators in the habitat selection process, at this macrohabitat level such selection and the potential range of variation of the habitats utilized may be more strongly

subject to genetic programming and imprinting, and basic habitat propensities may be shaped by natural selection through competition, predation and coevolution.

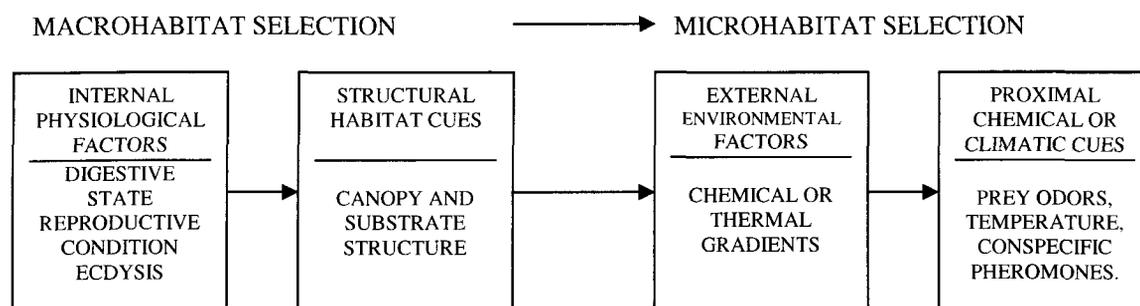


Figure 2.1: Proposed model of the habitat selection process in snakes by Reinert (1993).

Once a snake is in the preferred macrohabitat, site selection proceeds through the evaluation of relevant environmental gradients. Final microhabitat site selection is based upon proximal chemical or climatic cues necessary to satisfy immediate physiological requirements.

2.1.6 Climate change and snakes

As we have seen, reptiles must avoid environments where temperatures are too cold or too hot because of their ectothermal condition. In addition, they are not able to disperse as easily as birds and the habitat through which they move must not be too dry or very abrupt (high mountains or highways) (Root and Schneider, 2002).

Ectothermic organisms regulate their body temperature by behavioural means and in general their distribution is limited by external temperature conditions (Spellerberg and Sawyer, 1999). Their body temperatures rise and fall with ambient temperature conditions but over a limited range and depending on environmental conditions, they can maintain a body temperature independent of the ambient temperature. Biophysical

ecology studies are contributing to an understanding of the geographic distribution of snakes and the impacts that climate change may have on them by clarifying the basis of the correlations between species ranges and temperature, especially at the latitudinal and altitudinal species borders. Three hypotheses exist for why temperature may constrain the ranges of snakes, and reptiles in general. The first hypothesis is that geographical limits occur where the snake's thermal tolerances are periodically exceeded and thus snakes cannot survive. A second hypothesis is that snakes would avoid areas where they would not be able to obtain sufficient amounts of energy within a year to reproduce. The last hypothesis is that they would stay away from thermal conditions that do not allow adequate time for juvenile development to take place (Peterson et al., 1993).

Few researchers have studied the direct effect of climate change on reptiles (Gibbons, 2000). The studies that exist suggest that reptiles with restricted distribution, such as some Australian lizards, will have serious problems facing global warming (Brereton et al., 1995). The greatest impact will probably occur on those reptiles that have temperature-dependent sex determination (Janzen, 1994). For these species, the sex ratio of the hatchlings is determined by the temperatures that occur during the incubation period. Altered sex ratios could affect population demography and persistence (Gibbons, 2000). Additional studied effects of warming on some reptiles include enhanced juvenile growth rates and earlier ages of maturity (Frazer et al., 1993).

Furthermore, as the climate changes, the character of extreme weather events, such as droughts, will also change (IPCC, 2001), necessitating that animals adapt to relatively rapid changes (Parmesan et al., 2000). Rapid movements by birds are possible because they can fly, but for reptiles migration to new areas is much more difficult.

Hence, many more extirpations and even extinctions are probable in snakes than in birds because the climate changes could proceed more rapidly than the slow dispersal abilities of most herpetofauna, even without considering the additional difficulties associated with human land-use changes disturbing their migration paths (Root and Schneider, 2002).

2.2 The relationships between climate and species

In the absence of genetic change as a possibility for adaptation, populations have three possible responses to climate change: expand, decline, or go extirpated (or extinct). If local climate change improves the suitable habitat (e.g. removing abiotic or biotic barriers to occupancy), populations can expand in range or increase in density. Alternatively, if local climate change impacts a species negatively, populations can decline or individuals can disperse from negatively affected habitats to less-affected areas (including unoccupied sites or areas that were uninhabitable before climate change). Declines can also lead to extinction, particularly in those species with limited dispersal abilities or restrictive habitat requirements (Hellmann, 2002), or where an isolated acceptable habitat becomes unacceptable.

2.2.1 Species range

For a species to maintain its population size, its individuals must survive and reproduce. Particular combinations of environmental conditions are necessary for individuals to tolerate the physical environment, obtain energy and nutrients, and avoid their enemies. The total requirements of a species for all resources and physical

conditions determine where it can live and how abundant it can be at any place within its range. These requirements are termed the ecological niche.

2.2.1.1 The ecological niche

Hutchison, in 1958, suggested that the niche could be viewed as a multidimensional hypervolume in which each dimension would represent the range of some environmental condition or resource required by the species. Thus, the fundamental niche of a species would be the total range of physical environmental conditions suitable for its existence, while the realized niche would describe that part of the fundamental niche actually occupied by the species (Brown and Gibson, 1983).

Although we can recognize niches unmistakably only when organisms live in them, it is clear that there must be empty niches that are suitable for the species. The models developed in this study will show evidence of those suitable but non-occupied areas. Why do not species occupy those suitable but unfilled areas? Species may occupy only part of the suitable niches because, on the one hand, their limited capacity for dispersal may prevent a population from colonizing a non-contiguous area. On the other hand, the local limits of a species' range may be determined by immediate ecological factors that prevent local populations from expanding to adjacent suitable areas to which they would appear to have ready access. In these latter cases, the limiting factors that determine the boundaries are not obvious for the majority of species; at some point in an apparently gradual gradient of temperature, moisture, vegetation density or other environmental factors, the species no longer occurs.

Hutchinson's concept of multidimensional hypervolume gives an idea of the difficulties in explaining the factors that influence species' geographical ranges. Probably, climate is the major factor for the general limits of most living things. Just how organisms relate to the elements of climate, however, is not easy to establish, partly because the importance of climate may vary with the life cycle or between individuals. The relationships, furthermore, are often complex and are affected by non-climatic factors (Laubenfels, 1970). For example, a species may become increasingly restricted to low elevations and south-facing exposures as they approach the northern limits of their ranges, suggesting that their distributions are determined by temperature. However, the species could be restricted not by their inability to tolerate low temperatures directly, but by competition from species that are superior in cold climates (Brown and Gibson, 1983). For example, in Spain the European whip snake (*Coluber viridiflavus*) is present only in the Pyrenees; this fact could lead to the conclusion that the species is restricted to alpine and cold climates. However, it is widely distributed in Italy where it is a very common species. Hence, its Spanish distribution could be limited more by competition with the Montpellier snake (*Malpolon monspessulanus*) than by other environmental variables (Santos et al., 2002). Therefore, interpretations of factors influencing species' ranges must be done carefully and take into account as much information as possible.

Explanation of a simple biotic distribution pattern can be highly complex because there are many factors that are relevant to why an organism occurs in one area and is absent from another.

2.2.1.2 Organisms' tolerance limits: Shelford law

In 1913, V.E. Shelford developed the “Shelford law” which stated that organisms have ecological minimum and maximum limits of tolerance (Spellerberg and Sawyer, 1999). A species' tolerance curve represents the efficiency of operation of that organism (Figure 2.2). Some species have narrow limits of tolerance to some abiotic factors (stenotopic) and others have wide limits of tolerance (eurytopic). The geographical limit would be reached at the limit of performance of the species for a particular environmental variable (such as annual temperature or annual precipitation).

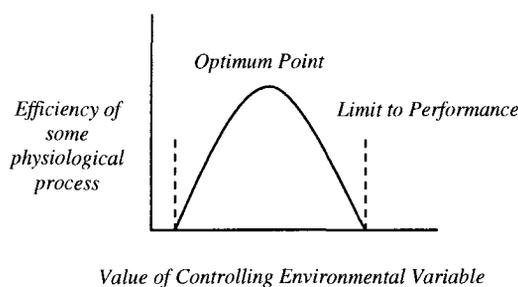


Figure 2.2: An example of Shelford law, showing a species tolerance curve (Adapted from Spellerberg and Sawyer, 1999)

2.2.1.3 Climate and species geographic range

As discussed, temperature is probably the climatic variable that has most influence on species' range limits. Although there are not many studies that establish a direct physiological or experimental connection between temperature and geographic range boundaries, there are many strong correlations between temperature isotherms and species' range limits (e.g. Root, 1998).

These patterns imply a general model of range limits based on the relationship between temperature and physiological tolerance. Following Liebig's law of the minimum (biological processes are limited by the single factor that is in shortest supply

relative to demand or for which they have the least tolerance (Brown and Gibson, 1983)). An organism's performance or fitness is expected to vary as a Gauss-bell function of temperature, driven by the relationship between temperature and the efficiency of underlying physiological processes (Huey and Kingsolver, 1989). Optimal performance occurs in the middle-part of this temperature range. At high and low temperatures, there are critical limits beyond which an organism is no longer able to reproduce successfully. As shown in Figure 2.3 A, these upper and lower critical limits are thought to set the geographic boundaries of a species' range (see further details in Section 2.2.2.3). The same pattern could also be applied to other environmental variables such as precipitation or radiation, depending on the requirements of the species. However, Austin (2002) indicated that there is not enough evidence that the frequency distribution of responses is always bell-shaped, and pointed out that this response may take a wide variety of shapes from skewed to bimodal.

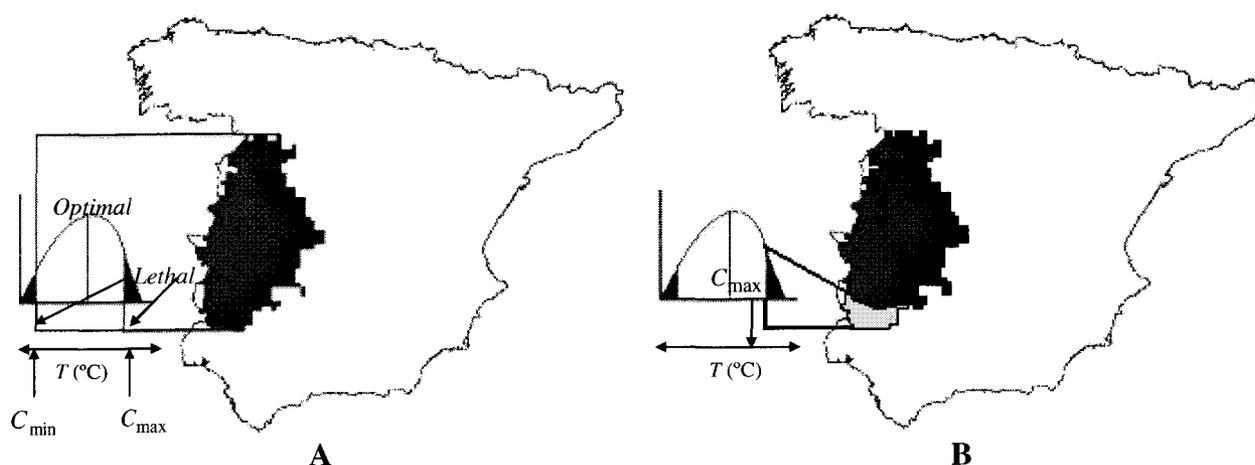


Figure 2.3: A simple model relating temperature and the geographic range of a hypothetical species in Spain. In figure A the geographic limits are set by a critical minimum (C_{\min}) and maximum (C_{\max}) temperature, beyond these limits the species is not able to survive. In Figure B, a temperature increase occurs and populations near the southern limits disappear (Adapted from Sanford, 2002).

2.2.1.4 Environmental gradients

Austin (2002) discussed the ecological causality of various types of predictors commonly used to predict plant or animal distributions and defined three types of ecological gradients, namely resource, direct, and indirect gradients.

Indirect gradients are those where the variable has no physiological relevance for a species' performance. Examples are slope, elevation, or elevation range. Their correlation with species distribution is due to their location-dependent correlation with variables such as temperature or rainfall (Austin, 2002). Elevation, for example, usually has an indirect effect on animal distribution by determining microclimate, of which some parameters, like *minimum winter temperature*, have a direct effect on species' survival and can thus impose strong distributional limits (Guisan and Hofer, 2003). Direct gradients are environmental parameters that have physiological importance, but are not consumed. Examples are temperature and soil pH for plants. Resource gradients are based on those variables that are consumed by animals, such as food or water.

Furthermore, an environmental variable (gradient) may be either proximal or distal, depending on its position in the chain of processes that link it to its impact on species (Austin, 2002). Indirect gradients would be distal variables. Models based on them will have only local value. On the other hand, the most proximal gradients will be the causal variable determining the species response. Models based on them will be the most robust and most widely applicable but the least practical in terms of knowing what to measure and in obtaining the measurements.

2.2.2 Climate change and species' geographic range

Many recent studies have documented changes in animal and plant distribution or phenology associated with climate change (e.g. Parmesan, 1996; Pounds, 1999; Kiesecker, 2001). Nonetheless, a gap exists between observations of an association between distributions and various environmental factors, and a mechanistic understanding of what physiological, ecological, and evolutionary processes maintain range edges (Hoffmann and Parsons, 1991). Understanding the true underlying mechanisms is crucial for predicting the biological outcomes of a changing climate (Crozier, 2002).

There are certain factors that influence whether a species will respond to climate change by moving towards new climatically favourable areas. Those factors include the availability of suitable habitat, the existence of physical or biological barriers to the dispersal of the species, the reproductive success of the species, the time taken for an individual of that species to reach reproductive maturity, the mobility of the species (Hughes et al., 1996), and the competition with other individuals. The ability of species to respond to climate change and shift habitat will also vary depending on the rate and nature of climate change (Spellerberg and Sawyer, 1999).

2.2.2.1 Scale issues and chance effects

Prediction of specific biogeographical consequences of climate change requires understanding how the borders of species' ranges depend on climatic conditions. Current understanding of this relationship is limited by the "scale gap" (Root and Schneider, 1995). An average increase in global mean temperatures is a landscape-scale prediction

based on climate models using 500 x 500 km grids (Schneider, 1993). These climate model predictions apply to “the big picture” of a species’ range: large-scale patterns of abundance and distribution. Analyses of distributions at this scale show that combinations of temperature and precipitation criteria are frequently good predictors of species’ ranges (Currie, 2001; Kerr, 2001). This association suggests that a change in environmental conditions may lead to a corresponding change in species’ ranges.

However, large-scale correspondence cannot differentiate between relevant and irrelevant environmental associations. There are a large number of potential environmental variables that may associate with species’ ranges by pure chance effects. Many environmental factors are also correlated with each other confounding their relative importance for organisms (Dennis, 1993).

Furthermore, the microhabitat that most animals occupy within the macrohabitat could buffer them from extreme fluctuations in environmental variables. Standard meteorological techniques recorded at long-term weather monitoring stations typically do not measure the conditions of the actual habitat where most animals live. It is these standardized measurements, however, that are most often used to assess the importance of climate for range limits (Crozier, 2002). Consequently, analysis of distributional effects of climate change when large-scale measurements are included should be interpreted carefully.

2.2.2.2 Lag issues and species’ interactions

Considerable evidence suggests that physiological optima and critical limits are likely to vary among species and within species of the same community. Assuming these

individualistic responses apply broadly to most species, climate warming is likely to shift species' ranges independently of one another, and disassemble present-day communities, leading to a new reorganization of the system, with new associations and interactions that are very difficult to predict (Crozier, 2002).

Changes in plant ranges will probably have dramatic effects on animals, both on the large biogeographic scale and on the local scale. The ranges of many animals are strongly linked to vegetation. Consequently, the ranges of animals that rely on specific vegetation will change as the ranges of these plants shift, assuming that some other factor is not limiting these animals. If the climate changes more rapidly than the dispersal rates of plants, it could result in extensive animal extinctions in the south or downslope before individuals can disperse and become established in the north or upslope. Thus, the ranges of animals relying on these plants could become compressed, and in some instances, both the plants and animals could become extinct (Root and Schneider, 2002). For example, the European whip snake (*Coluber viridiflavus*) has been associated with oak groves (Santos et al. 2002). Warming temperatures could lead this snake to move upwards in elevation. However, there could be a lag between migration of the snakes and of the oak groves that could lead to the species' extinction if they are not able to adapt to a new type of ecosystem.

Analysis of multiple pollen types from the last Ice Age (Wright et al., 1993) showed that, during the transition from that period to the present interglacial, nearly all species moved north. However, during a significant portion of the transition period, the distribution and combinations of pollen types showed the existence of associations that are not analogous to today's vegetation communities (Overpeck et al., 1992). That is,

whereas all species moved, they moved at different rates and directions, not as groups. Consequently, the groupings of species during the transition period were often dissimilar to those present today. Therefore, it is expected that in the future, ecosystems will not necessarily move as a unit as climate changes (Root and Schneider, 2002).

Climate change may also impact local populations by altering the strength of interactions between a species and its competitors, mutualists, predators, prey, or pathogens (Lubchenco et al., 1991). For example, following a slight temperature increase, an individual that was previously living near its physiological optimum may be forced to spend more time operating at a reduced level of performance. Such sublethal effects may change the way that one species interacts with another by changing competitive ability, rates of consumption, or susceptibility to predators or pathogens. Moreover, these effects may occur throughout a species' range, not just in populations living near range boundaries (Sanford, 2002). Furthermore, some animals may no longer be able to coexist because an invading species disrupts the balance between competing species or between predator and prey (Root and Schneider, 2002). For this reason, it is important to understand not only the direct impacts of climate change on a species of interest, but also how species may be indirectly affected via impacts on other community members (Hellmann, 2002).

2.2.2.3 Distributional change

Every species has an optimum region within which it shows greater development, a larger number of individuals, and above all, better fulfilment of its life cycle. Near the frontiers the cycle often begins to weaken, to be interrupted, or is slowed down

(Dansereau, 1957). Often, central populations in the core of a species' range tend to have the highest abundance; population sizes at the edges of a range are often smaller and more variable than those at the core. This phenomenon may place edge populations at greater risk of extirpation than core populations (Brown, 1984).

Given this model, a species' range contracts when an environmentally limiting factor (e.g. temperature) changes and eliminates populations living at the margin of the range. For example, a population living near its southern boundary may disappear when temperature increase pushes individuals beyond their upper critical limit. As shown in Figure 2.3 A, the geographic limits of a hypothetical sedentary species living in Western Spain are set by a critical minimum (C_{\min}) and a critical maximum (C_{\max}) temperature, beyond which the organism is unable to successfully reproduce (shaded regions under curve).

In Figure 2.3 B, a temperature increase occurs throughout the geographic range. Individuals near their southern range limit experience a higher temperature that exceeds the species' upper critical range. Individuals are unable to successfully reproduce, and southern populations ultimately disappear. Analogous processes may expand the northern range limit, leading to a northward shift in the entire range (Sanford, 2002).

Nevertheless, little is known about range edge populations and how they may differ from central populations (Hoffmann and Parsons, 1991). Little is known, for example, about the extent to which marginal populations are locally adapted, whether they are more likely to be extirpated than equal-sized central populations, or what percentage of edge populations experience demographic marginalization and are dependent on migration from central populations for persistence. In these edge

populations, there may be trade-offs between stress tolerance and fitness (Bradshaw et al., 1998) such that migration from central-range populations opposes local edges adaptations (Kirkpatrick and Barton, 1997). Thus, population-level and species-level processes could interact with a physiological process to define a range limit (Crozier, 2002).

2.2.2.4 Climate change and corridors

When the climate changes, many species may be affected similarly, and they may disperse synchronously along the same routes if the conditions along these routes meet their requirements for survival. In 1940, Simpson defined a corridor as “a route that permits the spread of many or most taxa from one region to another” (Brown and Gibson, 1983). From this point of view, a corridor would allow the movement from a source area to another suitable area so that both areas would obtain elements representative of the other. However, in the context of climate change the idea of corridor might be modified to indicate a recognition of the need of species to move spatially as a response, leaving the source area behind and extending to a new area (Birnie, 2001). The signal of the movement will be unidirectional instead of bidirectional as the usual theory of ecology recognizes.

The synergistic effects of habitat fragmentation and climate change represent one of the most potentially serious global change problems. During the Pleistocene Ice Age, many species survived by migrating to appropriate habitats (Root and Schneider, 2002). Today such migrations would be much more difficult because they would involve migration across freeways, agricultural zones, industrial parks, and urban areas which

would seriously interfere with or eliminate the contiguity and continuity of potential migration corridors. Huge artificial corridors have been proposed to allow the movement of the species; however, as Hobbs and Hopkins (1992) recognize, the utility of these corridors in counteracting the effects of climate change is uncertain.

2.3 Predicting species distributions

In this section, the most common approximations used in habitat modelling are identified and the uncertainties that these kinds of studies usually have are described. The main focus is on logistic regression, the method adopted.

2.3.1 Model formulation

Science is the game of prediction; nonetheless, nature is too complex and heterogeneous to be predicted accurately in every aspect of time and space from a single model. A perfect model has been defined as the one that is able to describe with precision the reality and that can be applied in many different situations. That is, the three desirable model properties are: generality, reality, and precision. However, usually models only are able to fulfil two of these characteristics. This trade-off allows a distinction of three groups of models (Guisan and Zimmermann, 2000):

Analytical models form the first class. They would be focused in generality and precision but they can predict a limited reality. An example of this model is the Lotka-Volterra equation, which describes the predator-prey interaction in an ecosystem. A second group would be the mechanistic models. They are designed to be realistic and general and they base their predictions on real cause-effect relationships. The third group

encompass the statistical models, which sacrifice generality to be precise and real. Statistical predictive distribution models such as the one used in this study are generally categorized as empirical models (Guisan and Zimmermann, 2000).

Predictive distribution models, predictive habitat models, ecological niche models, habitat suitability models, niche-based models, or biogeographical distribution models are all terms used in the literature to describe models that are designed to map the distribution of species when their presence or presence/absence is related to environmental factors. The general approach of these tools consists in looking for statistical relationships between the species and a series of independent variables and using these relationships for predicting the probability of species presence or absence at spatial or temporal unsampled locations. As Guisan et al. (2002: 91) indicated the goal of these techniques is to find “a model that predicts the ecological attributes of interest from a restricted number of predictors. The concept of parsimony, that the simplest explanation is the best, is inherent in such modelling efforts”.

These kinds of model have become increasingly popular in recent years because, among other reasons, the projection of the functions generated to areas where environmental factors are known but species have not been sampled is a cost effective method to map possible species distributions (Brotons et al., 2004). These projections can be applied to model species distributions, either in time (to assess the impact of future climate or land use change) or in space (to establish endangered species ranges and protect their habitats).

Most of these models can be classified as correlative, as they rely on strong links between distribution records and environmental predictor variables to make predictions.

Correlative models can be separated into two groups. Models that use presence/absence records have been termed as group discrimination techniques and those that use only presence records have been termed as profile techniques (Robertson et al., 2004). A major difference between both techniques is the quality of data needed. Group discrimination techniques include generalized linear models (within which logistic regression, the model used in this study, is included), generalized additive models, classification and regression tree analysis, and artificial neural networks. These methods require good quality presence/absence data in order to generate statistical functions that predict the habitat suitability if the species presence/absence is based on the explanatory variables (Brotons et al., 2004).

At present, the most popular habitat-suitability models are generalized linear models. Evaluation between them has indicated that they have relatively similar predictive success, but factors such as species abundance and data quality have a strong influence on model performance (Manel et al., 1999). In this vein, Lewis (2004: 305) studied artificial birds' nests and compared a variety of generalized linear models, finding that "logistic regression was the most appropriate and flexible statistical test for analyzing binary datasets".

2.3.2 Overview of logistic regression

Logistic regression has been broadly applied in ecology and, as was discussed above, it is becoming very popular in modelling species distributions. Examples include the use of logistic regression to predict the distribution of plants (e.g. van Horssen et al., 2002), molluscs (Berg et al., 2004), insects (e.g. Cowley et al., 2000), fish (e.g. Rieman

and McIntyre, 1995), amphibians (e.g. Teixeira and Arntzen, 2002), reptiles (e.g. Guisan and Hofer, 2003), birds (e.g. Brotons et al., 2004), and mammals (e.g. Carrol et al., 2004).

Logistic regression relies on the logistic function shown below.

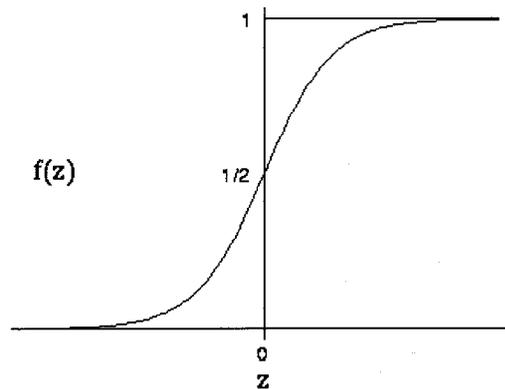


Figure 2.4: The S-shaped function or logistic function

The function is given by the equation:

$$[2.1] \quad f(z) = \frac{1}{1 + e^{-z}}$$

Equation [2.1] is shaped as an elongated "S" (Norusis, 2003) as shown in Figure 2.4.

At $z = 0$ the function is $1/2$, as z decreases the function decreases to 0, and as z increases the function increases to 1. Therefore, the function takes values between 0 and 1.

The variable z is viewed as representing an index that combines contributions of several independent variables or predictors and the logistic function denoted $f(z)$ represents the probability of the dependent variable or outcome for a given value of z .

In this study, I am interested in the impact of climate on the presence or absence of particular species of snakes, for example, the Asp viper (*Vipera aspis*). Therefore, the distribution of this species represents the outcome by a value of 1 for presence and by 0 for absence. The independent variables could be selected from a set of climatic and topographic variables. In logistic regression, the parameters of the model are estimated using the maximum-likelihood method. The coefficients that make the observed results most likely are selected. Because the logistic regression model is nonlinear, an iterative algorithm is necessary for parameter estimation (Norusis, 2003). Once the logistic regression is run, the predictors showing strongest correlations within the environmental dataset could include annual precipitation, maximum spring temperature, and minimum winter temperature.

To obtain the logistic model from the logistic function we can write z as the linear sum of: $z = \alpha + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_i X_i$ just as in linear multiple regression. So we can think of z as an index that combines the X s (explanatory variables).

Now we substitute the linear sum into the logistic function:

$$[2.2] \quad \pi = P(\text{Outcome} = 1 | Xs) = f(z) = \frac{1}{1 + e^{-(\alpha + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_k X_k)}}$$

Equation [2.2] has the same form of equation [2.1] and therefore varies similarly to the sigmoidal curve (the S-Shaped curve) shown in Figure 2.4. It is describing the probability of the outcome value equal to 1 (the species is present) as the explanatory variables, X s, vary.

A function having this form is called a “logistic regression function”. The coefficients, α and β_i , have been estimated to define the model with the maximum-likelihood method.

For example, it could be desirable to use the X_s to describe the probability that the Asp viper is present in some area. In the example:

Outcome= Asp viper (1 = presence, 0 = absence)

X_1 = Annual Precipitation

X_2 = Maximum Spring Temperature

X_3 = Minimum Winter temperature

In the current research the dataset is constituted of 4945 cells with values of presence/absence of the species on which the X_s variables have been measured. Suppose the results of the model fitting yield the following estimated parameters:

$$\alpha = 19 \qquad \beta_1 = 0.002 \qquad \beta_2 = -1.8 \qquad \beta_3 = 1.7$$

If the predictions of the climate variables X_1 , X_2 , X_3 , for a projected scenario of climate change is implemented, the estimate for the probability of the presence of *Vipera aspis*, at a site with 300 mm of annual precipitation, 28°C of maximum spring temperature and -1°C of minimum winter temperature is:

$$\Pi = P(\text{Outcome} = 1 | X_s) = 0.32$$

It can be concluded then that the model predicts that the Asp viper will not be very likely to be present at that particular site in the future projected scenario.

2.3.2.1 Logit transformation

Instead of estimating α and β_i from equation [2.2], the form of the dependent variable can be changed from π to $\text{Ln}\left(\frac{\pi}{1-\pi}\right)$. This is called logit transformation of π (Norusis, 2003).

$$\text{So: } \frac{\pi}{1-\pi} = \frac{\frac{1}{1+e^{-(\alpha+\beta X)}}}{1-\frac{1}{1+e^{-(\alpha+\beta X)}}} = e^{(\alpha+\beta X)}$$

The transformed dependent variable, called logit, is then expressed as:

$$[2.3] \quad \text{Ln}\left(\frac{\pi}{1-\pi}\right) = \text{Ln}\left(e^{(\alpha+\beta X)}\right) = \alpha + \beta X .$$

Odds of the outcome variable equal to 1 is defined as the ratio of the probability of the outcome equal to 1, π , to the probability of the outcome not equal to 1, $1-\pi$.

Thus,

$$[2.4] \quad \text{Odds}(\text{Outcome} = 1) = \frac{\pi}{1-\pi}$$

The larger the odds ratio, the stronger the relationship, meaning the higher the ratio of success versus failure for those in that category compared to the reference category.

To calculate the odds ratio, the logistic model needs to be written in logit form.

$$[2.5] \quad \text{Logit}P(\text{Outcome} = 1|Xs) = \text{Ln}\left(\frac{P(\text{Outcome} = 1|Xs)}{1 - P(\text{Outcome} = 1|Xs)}\right)$$

In the previous example $P(\text{Outcome} = 1|Xs) = 0.32$, so

$1 - P(\text{Outcome} = 1|Xs) = 0.68$. Dividing 0.32 by 0.68 and taking the natural logarithm yields 0.47.

With regard to the odds, we often want to consider what happens to the logit when only one of the Xs varies while the others are fixed. For example, we might want to know what happened to the logit when maximum spring temperature and minimum winter temperature are fixed and annual precipitation changes from 300 mm to 800 mm. To answer this question the model in logit form is written as:

$$\alpha + \beta_1 ANNP + \beta_2 MaST + \beta_3 MiWT$$

So,

$$\begin{aligned} & \text{logit } P(\text{Outcome} = 1|ANNP = 300, \text{ other } Xs \text{ fixed}) - \text{logit } P(\text{Outcome} = 1|ANNP = 800, \text{ others } Xs \text{ fixed}) \\ = & \alpha + \beta_1 ANNP(300) + \beta_2 MaST + \beta_3 MiWT - (\alpha + \beta_1 ANNP(800) + \beta_2 MaST + \beta_3 MiWT) \\ = & \beta_1 \end{aligned}$$

So, β_1 represents the change in the logit or log odds due to the annual precipitation when all the other variables are fixed. If a similar operation is performed with other variables, β_i represents the change in the log odds that would result from a one unit change in the variable X_i , when all other Xs are fixed.

2.3.3 *Uncertainties of habitat modelling*

Although logistic regression is a popular statistical technique in ecological modelling, there are still many unsolved research issues (Ryan, 2000).

2.3.3.1 Logistic regression uncertainties

Ryan (2000) states three main problems when using logistic regression. First, the difficulties of developing a suitable coefficient of determination (R^2). Second, the possibility for poor results produced by the method of maximum likelihood to fit the model. Third, the challenge of developing suitable graphical techniques.

Regarding the R^2 , there is little agreement about which R^2 -type should be used. In ordinary multiple regression analysis, there is a general consensus on its use as a measure of how strongly the independent variables are related to the dependent variable. However, in logistic regression analysis, there is as yet no consensus on how the corresponding measures of the strength of association between the dependent variable and the total set of predictors should be calculated (Menard, 2000). If we simply use the linear regression form of R^2 (R_O^2) when the response is binary, a value close to zero is obtained even when the model fits the data very well (Ryan, 2000). Various alternative R^2 -type statistics have been proposed. Menard (2000) for example, examined different R^2 for continuous predicted values (R^2 analogs) that are generally used when applying logistic regression: The ordinary least squares R^2 (R_O^2), which is the R^2 used in multiple regression analysis; the log likelihood ratio R^2 (R_L^2); the geometric mean squared improvement per observation R^2 or Cox and Snell R^2 (R_M^2); the adjusted geometric mean squared improvement R^2 or Nagelkerke R^2 (R_N^2); and the contingency coefficient R^2 (R_C^2). Menard found that all these could be reasonably used to compare models, with the exception of R_O^2 , because it may decrease when additional variables were added to the model.

Regarding the problem with the method of maximum likelihood, most statistical packages available apply this technique when estimating the parameters of the logistic model. However, it has been demonstrated that it can produce poor results in terms of p-values and confidence intervals for the estimated coefficients (β_i), especially for small and sparse data sets and/or when the average value of $f(z)$ (Figure 2.4) is close to either zero or one. Another method called “exact logistic regression” was suggested by Cox (1970). However, as Ryan (2000: 2025) recognized, “an exhaustive study of exact logistic regression vs. maximum likelihood is apparently yet to be performed”.

2.3.3.2 Measurement errors

When habitat suitability models are applied, measurement errors influence the performance of the models. Measurement errors arise from imperfections in measuring equipment and observational techniques, and imprecision in computer processes. Errors include the following: a whole population is rarely sampled; some individuals may be unintentionally sampled more than once; and locations may be recorded inaccurately (Elith et al., 2002).

The vast majority of habitat models that use presence-absence as a response variable have assumed that if a species occurs at a site, it will be detected. This assumption has the effect of equating detection probability to one. Failure to detect a species at occupied sites can lead to poorly formulated habitat models and thus to erroneous prediction of a species response to habitat change (Gu and Swihart, 2004). Furthermore, if uncertainty exists in the base data, this uncertainty could be propagated as the data are summarized, classified, modelled and interpolated when a GIS tool is

applied. Other sources of measurement error in predictor variables include translation of vector data into raster format, and uncertainty about exact location of polygon boundaries for data (Elith et al., 2002).

2.3.3.3 *Systematic errors*

Systematic error occurs as a result of bias in measuring equipment, sampling procedures or GIS operations. As Elith et al. (2002: 315) pointed out, “this kind of error is difficult to treat and correction factors may introduce further biases if the direction and magnitude of the error is unknown”.

Also, predictor variables can be biased. As the grain at which data are recorded becomes coarser, units that exist at a finer grain are subsumed into more prevalent ones, leading to bias against unusual classes. Uncertainty may also be spatially clustered, such as errors in a digital elevation model (DEM), which may be globally small but locally large and spatially correlated. Furthermore, environmental variables are frequently spatially autocorrelated, such that sites in close proximity are more similar than sites separated by greater distances (Knapp et al., 2003). Therefore, the hypothesis of independence is not always satisfied. Spatial autocorrelation is an issue with which most habitat modellers have to deal. It presents problems for statistical testing because most relevant statistical models assume independence of error terms. Consequently, when developing models without taking into account spatial autocorrelation, error terms are underestimated, leading to over-optimistic estimates of the test statistics (Fielding and Haworth, 1995).

2.3.3.4 Biotic errors

Biotic errors arise because not all of the ecologically relevant processes have been specified in the model. Good predictions would require knowledge of all the underlying causal mechanisms of species occurrence at very refined temporal and spatial scales and full understanding of the ecology of the species. If all causes of variation were known and could be quantified, prediction would be certain and “present” or “absent” would be the only necessary predictions from presence-absence data. Because it is impossible to make error-free predictions, usually predictions are made in terms of the chance of occurrence (Elith et al. 2002).

Models used to predict species presence are based on observations of current distribution, and in a strict sense, predictions are estimates of the probability that the species currently occupies a site. Within a dynamic population, it is not always clear whether some of the current absence records are actually records of unsaturated but suitable habitat. The problem of unsaturated population must be also taken into account when habitat models are developed. There is an implicit assumption in most presence/absence designs that breeding habitats are saturated, but this assumption may be unjustified. Therefore the possibility that the population could be unsaturated must be taken into account when recording the presence data and, when developing the model, it must be recognized that areas where the species has not been recorded could be suitable for its survival. In addition, individuals of a species may not congregate in the most suitable locations because of behaviour, competition, or dispersal dynamics (Elith et al. 2002).

Although presence records can be assumed to be reliable, the same cannot be said for absence records; indeed, failing to detect a species does not guarantee that the species is absent. Presence is a probabilistic function mainly affected by species abundance and detectability (Brotons et al., 2004). As these researchers stated (Brotons et al., 2004: 439), “the assumption that absence indicates areas where species are not present due a negative species-environmental relationship is not necessarily a valid one”, since habitat population dynamics, fragmentation, rate of dispersal or history, may induce species absence from otherwise optimal habitat (Araújo and Williams, 2000). If the role of such events is significant and the species is not in equilibrium with its environment, inaccurate absence data may affect the model building process.

2.3.3.5 Scale problems

Any output derived from an ecological study depends on the scale at which it is viewed. Patterns that are obvious at a particular spatial scale may change at finer or broader scales. Consequently, statements about habitat relationships are of very limited value unless they are accompanied by qualifiers explaining the scale of measurement adopted (Wiens, 2002). Furthermore, when habitat models are designed, different scales of study might be adopted depending on the organism that is being modelled. The spatial scale is usually established by *grain* (the finest scale of resolution of the data) and *extent* (the area to which a model is applied). *Grain* and *extent* define the window through which patterns are recognized (Wiens, 2002). Failing to detect an appropriate scale of study might lead to erroneous conclusions about the relations between the species and predictors.

CHAPTER 3

DATA AND METHODS

The distributions of many plant and animal species have been modelled recently, yet little research has predicted future reptiles' distributions (Guisan and Hofer, 2003). The purpose of this study is the application of logistic regression to predict the future distributional patterns of snakes within the Spanish Iberian Peninsula, an area where the potential effects of climate change on the distributions of reptiles at the population level have been inadequately studied.

In this section, the data and the methods used in their preparation and analysis is described. First, the variables for the study are identified together with the different spatial adjustments and statistical tools that were used to prepare the data. In this process, the main goal was to produce at the same resolution maps acquired from different sources. Second, prior to the logistic analyses, the requirements that this kind of regression needs to fulfil were checked. Finally the overall process of model building carried out to produce the final models is described.

A GIS (Geographic Information System) is the best tool available for preparing and analyzing the spatial data sets used in this thesis. ArcGIS 8.2 (ESRI inc., Redlands, CA) was the GIS software used in the current research. Furthermore, GeoDa (University of Illinois, Urbana-Champaign, IL) was the software tool applied for exploring the spatial autocorrelation in the data. SPSS 12.0 for Windows (SPSS inc., Chicago, IL) was the statistical package used for producing the correlation matrix, principal component analysis and logistic regressions. Finally, the spreadsheet software Microsoft Excel 2003 (Microsoft corp., Redmond, WA) was useful for organizing and managing the data.

3.1 Environmental data acquisition and preparation

Data obtained from different sources had to be prepared prior to the analysis. The snake dataset had a 10 x 10 km resolution and this was selected as the standard resolution for other data sources. Consequently, recent climate, and topography maps with a 1 x 1 km resolution had to be upscaled, while climate change maps with a 56 x 56 km resolution were downscaled. Figure 3.1 summarizes the steps that were followed to acquire and prepare the climate and topography datasets.

3.1.1 Climatic data

Recent and future climatic data consisted of a set of raster and vector maps, respectively, unpublished data made available by the Instituto Nacional de Meteorología (INM) of Spain.

3.1.1.1 Recent climate

The climatic variables available for use in this climate change investigation are: annual precipitation, mean annual temperature, mean annual temperature range, and the precipitation and minimum and maximum temperatures occurring in spring, summer, autumn and winter. Months were aggregated into seasons, seasonal divisions being based on winter and summer solstices as well as vernal and autumnal equinoxes. Thus, January, February and March are classed as winter as spring begins on the 22nd of March. Next, April, May and June are spring as the beginning of summer is on the 21st of June. Similarly, July, August and September are the summer and October, November and December are the autumn.

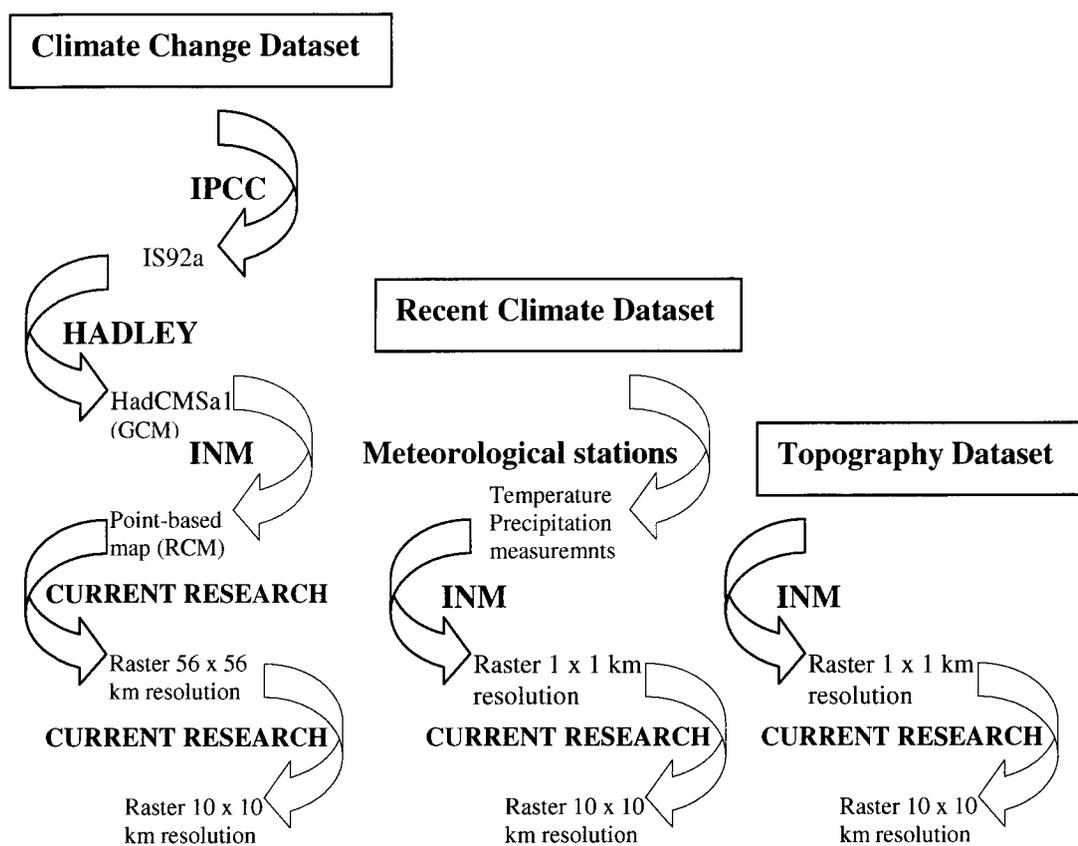


Figure 3.1: Overview of the steps followed during the data preparation phase and entities that made available these data.

DEM: Digital Elevation Model

HadCMSa1: Hadley Centre's general circulation model (GCM)

HADLEY: Hadley Centre, Exeter, Devon, U.K

INM: Instituto Nacional de Meteorología (National Institute of Meteorology), Madrid, Spain

IPCC: Intergovernmental Panel on Climate Change

IS92a: IPCC's emissions scenario

RCM: Regional circulation model

Furthermore, the mean annual temperature range was obtained by subtracting minimum winter temperature from maximum summer temperature.

The climate variables above were selected either because they have been shown to be important correlates of diversity gradients and/or of species distributions for at least some animal groups or because they have been hypothesised to be important for species (Hawkins and Porter, 2003).

The recent climate dataset is based on the thirty-year period between 1971 and 2000. One hundred and forty three main meteorological stations, 1504 thermometric stations and 4835 pluviometric stations were used to develop the maps. The INM applied kriging (Demers, 2003) to interpolate from the meteorological stations data to the 1 x 1 km grid.

3.1.1.2 Climate change scenario

The models obtained from relating current climate and topography to contemporary species distributions were used to project the species distribution onto a climate change scenario. These projections were carried out by changing the values of the predictor variables from current values to those of the climate change scenario and then rerunning the models to calculate the new potential distributions.

The scenario used in this study has been derived from climate models that include the best possible representation of processes in the atmosphere, ocean and land given present scientific knowledge and computing technology. Climate change model outputs should not be understood as indicating how much the climate will change by a certain time. Rather, they should be interpreted to be denoting the condition to which climate is tending (Kerri, 1999).

As shown in Figure 3.1 the future climate change scenario was obtained from the Instituto Nacional de Meteorología (INM) of Spain. The General Circulation Model (GCM) used was the HadCM2 (Hadley Centre Coupled Model v.2) for the period 1890-2100 from the Hadley Centre (U.K.). HadCM2 is a coupled atmosphere-ocean general circulation model described in detail by Johns et al. (1997) that has been used for a wide

range of climate change experiments. It has a spatial resolution of 2.5° latitude x 3.75° longitude, giving a grid of 96 x 73 cells for the whole Earth.

The refinement of the general circulation model by the addition of the emissions scenarios has the name of “climate integration”. The climate integration performed, called HadCM2GSA1, was based on an ensemble of greenhouse gases plus sulphate integrations. It assumed an addition of historic SO₄ from 1860 to 1989 and the IPCC’s IS92a emission scenario for the period 1990-2099 (CRU-UEA, 2005).

The IS92a scenario, a business-as-usual type scenario (Leggett et al., 1992) detailed in the 1992 Supplement (IPCC, 1992) to the IPCC First Assessment Report (IPCC, 1990); assumes a 1 % equivalent CO₂ increase per year since 1990, a population rise to 11.3 billion by 2100, an average economic growth of 2.3 % per year between 1990 and 2100, and a mix of conventional and renewable energy (IPCC, 1992).

General Circulation Models such as HadCM2 have a spatial resolution too coarse for the majority of impact assessments. As a result, a downscaling technique called “Analog” (Zorita and Storch, 1999) was applied to convert the outputs from the HadCM2Sa1 to a suitable resolution for the current application.

3.1.1.2.1 Climate change scenario for the Spanish Iberian Peninsula

According to Hulme and Sheard (1999) mean annual temperature over Spain has increased by nearly 1.6°C over the last century. The warmest years occurred in 1989, 1995 and 1997 (Figure 3.2). This warming has been greatest in the summer season (nearly 2°C) and least in the winter season (about 1.4°C). Iberia receives about one third of its precipitation during the December-February winter period. Figure 3.2 shows that

winter precipitation has been quite variable during the last century. Some severe winter droughts have also occurred in recent years, for example the winters of 1988/89, 1991/92 and 1992/93.

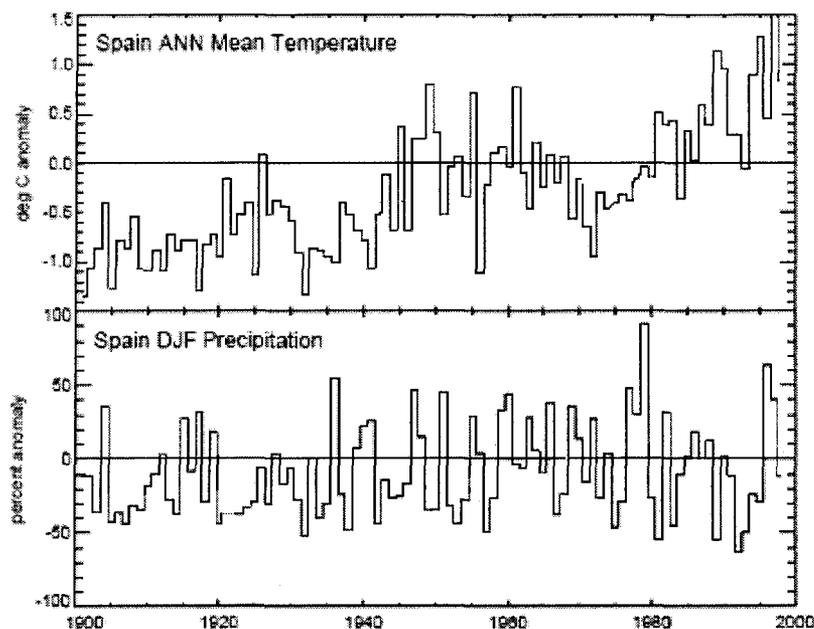


Figure 3.2: Changes in annual mean temperature, 1901-1998 (top), and winter precipitation, 1901-1998 (bottom), over Iberia. Changes are with respect to the average 1961-90 climate values of 13.1°C and 257mm respectively. Source: Hulme and Sheard, (1999)

As a consequence of the difficulties of downscaling a GCM to produce a reliable climate change scenario, a small amount of climate change data is available for the Iberian region. However, the climate change dataset used in this study is, to date, the most reliable that can be found with its high spatial resolution. Further research is required to improve the lack of consistent Regional Circulation Model (RCM) outputs in Spain.

The “Analog” method used to generate this climate change dataset is based on statistical techniques to improve the spatial resolution (downscaling), from the output of the HadCM2GSa1. In essence, “Analog” searches for empirical relationships between the

circulation patterns produced by the General Circulation Model and climatic variables measured at the surface by meteorological stations described with maximum resolution. According to Balairon et al. (2001) the validation process of this technique was reasonably consistent and showed small errors except for the autumn precipitation in the Levante area (central and south Mediterranean shore). In addition, these authors add that the experiment HadCM2Sa1 does not fit well the precipitation observed in Spain, and therefore conclusions derived from this variable should be carefully interpreted.

The final output of this procedure were three vector maps formed of 203 points (Figure 3.3) for annual precipitation and the maximum and minimum temperatures for each month for the period 2000-2099. Furthermore, mean annual temperature was calculated as the average of the maximum and minimum temperatures; winter precipitation was calculated as the accumulated precipitation in January, February and March; spring precipitation as the accumulated precipitation in April, May and June, summer precipitation as the accumulated precipitation in July, August and September and finally autumn precipitation as the accumulated precipitation in October, November and December.

Years in which species distributions are usually projected in the literature include 2020, 2050 and 2080 (e.g. Harley and Dawson, 2000; Currie, 2001, Peterson et al., 2002, Thuiller, 2003). The 2020 scenario was the one chosen to predict the future species distributions in the current study. Because the only scenario available for the current research was the IS92a from the Hadley Centre, and there were no other scenarios to make comparisons, it seemed more prudent to project the species distributions to a closer year where uncertainties and the range of variability among scenarios are smaller.

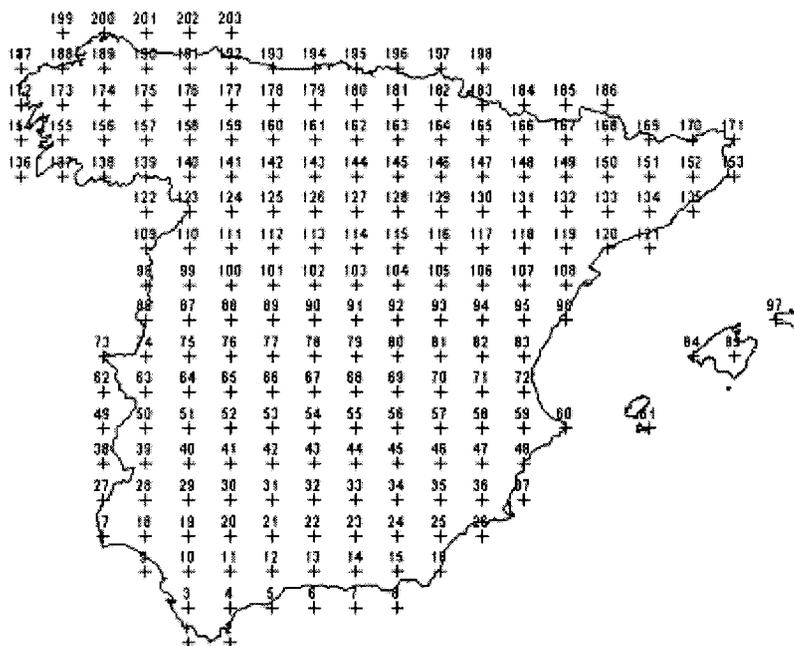


Figure 3.3: Two hundred and three reference points map as was obtained from INM (Instituto Nacional de Meteorología)

Figure 3.4 shows a comparison between the IS92a scenario and the family of SRES (IPCC, 2001). In 2020, there are subtle differences in global temperature change among them. All scenarios predict a global temperature increase. Projected surface warming trends for the IS92a and SRES-B1 are close to each other and show slightly lower global temperature change.

Because the climate change projections were available as a point-based map, it was necessary to transform them into the standard grid. As described in section 3.1.3 the standard grid was defined as the grid in which all the analysis were based. It has a 10 x 10 km (100 km²) resolution.

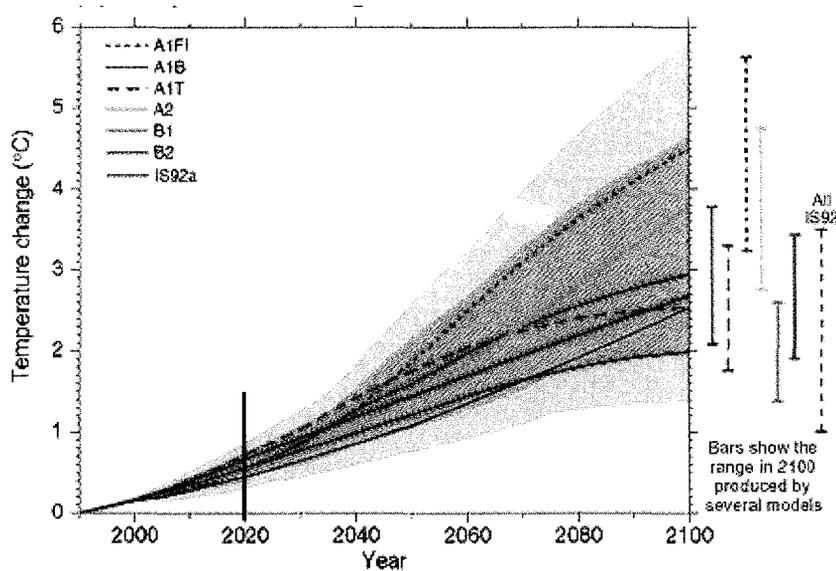


Figure 3.4: Global-mean temperature change associated with the IPCC scenarios: A1FI, A1T, A1B, A2, B1, B2 and IS92a. These figures have been derived using a simple climate model. The several models envelope shows the temperature projections for the simple model when applied to a number of complex models with a range of climate sensitivities. (Adapted from: IPCC, 2001).

As shown in Figure 3.5 (Steps A to B), the Hadley climate scenario was interpolated from point to raster by means of the Inverse Distance Weighting (IDW) method (Demers, 2003). A value $p=2$, the conventional weight adopted in this kind of interpolation (Lo and Yeung, 2002), was assigned to the IDW weight equation, assigning large influence to the values closest to the interpolated point. The result was a 56 x 56 km raster grid. This resolution was too coarse to be downscaled directly into the 10 x 10 km resolution. Consequently a previous refinement using the recent climate dataset was applied in order to obtain a finer resolution. Steps B to C of Figure 3.5 show this refinement process. Firstly, a neighbourhood statistic (Lo and Yeung, 2002) was applied to the recent climate map that upscaled it from a 1 x 1 km resolution to a 56 x 56 km resolution. Subsequently, the difference between future and recent climate grid in a 56 x

56 km resolution was calculated and added to the original recent climate map. A final smoothing procedure was applied to the grid to create the final climate change scenario.

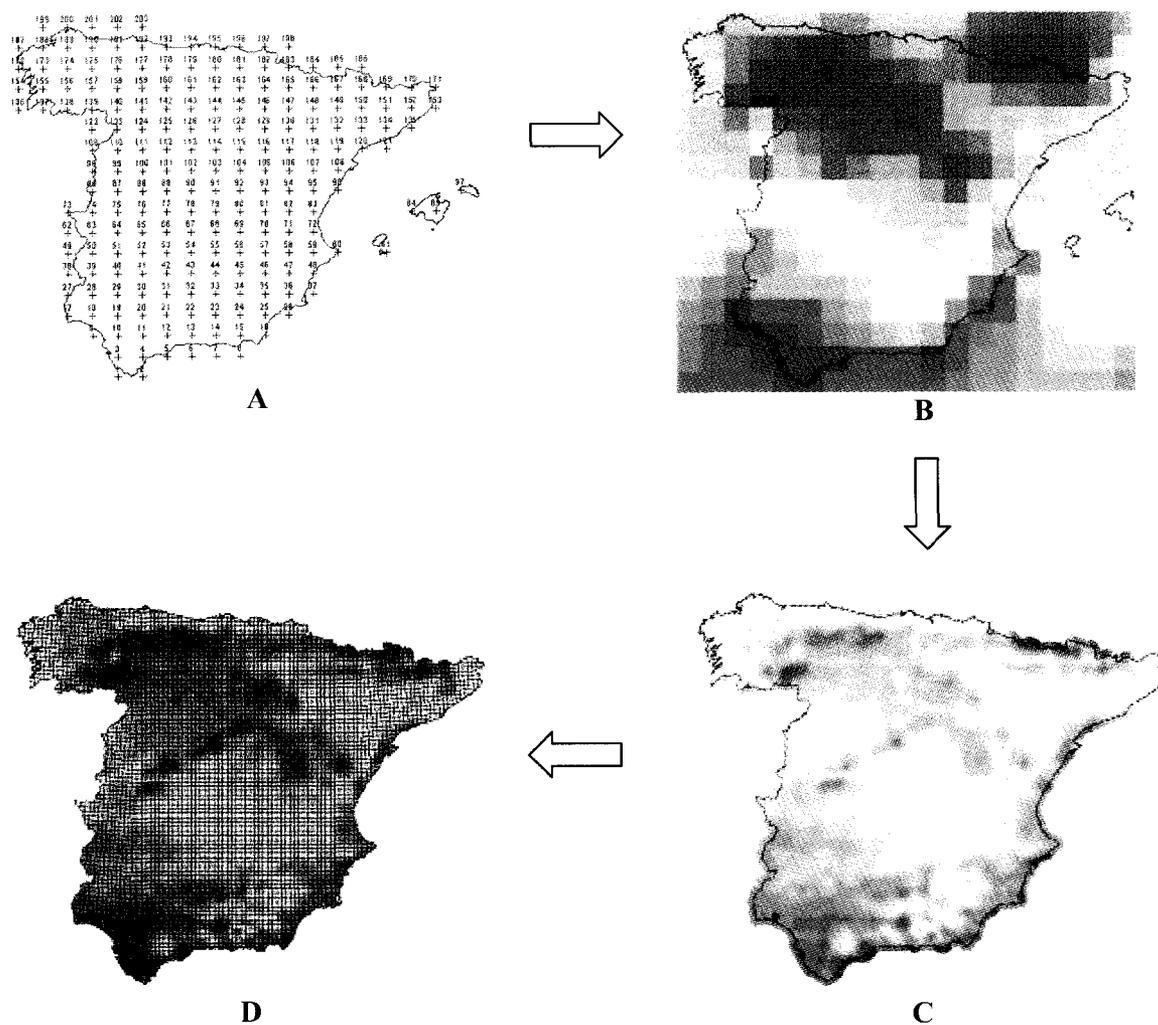


Figure 3.5: Diagram illustrating the transformation process of annual temperature scenario in 2020 from a point-based map (A) to the standard grid (D)

Finally, to bring the data to the standard grid 10 x 10 km resolution, recent climate, topographic and Hadley climate scenario maps, were upscaled from 1 x 1 km

resolution (Figure 3.3; Steps C to D) by applying a zonal statistic (Demers, 2003) after overlaying the standard grid on these maps.

3.1.2 Topographic data.

The mean elevation, elevation range, and mean slope of 1 x 1 km grid cell size referenced to UTM coordinates were used. These maps were derived from a digital elevation model (DEM) of the Spanish Iberian Peninsula available from the INM.

3.1.3 Snake data

The snake dataset was obtained from the “*Atlas y Libro Rojo de los Anfibios y Reptiles de España*” (Pleguezuelos et al., 2002). A previous edition (Pleguezuelos, 1997) had 78,000 records, which brought together all published data related to Spanish amphibian and reptile distributions until 1997 and additional records from museums and other herpetological collections. Production of the new atlas included a period of meticulous fieldwork that provided information on reptile and amphibian occurrence in previously un-surveyed areas (Pérez-Mellado, 2002). The 2002 atlas contains more than 200,000 records on 95 amphibians and reptiles, within which could be found the 13 snakes that were used in the analyses: *Coluber viridiflavus*, *Coronella austriaca*, *Coronella girondica*, *Elaphe longissima*, *Elaphe scalaris*, *Hemorrhois hippocrepis*, *Macroprotodon brevis*, *Malpolon monspessulanus*, *Natrix maura*, *Natrix natrix*, *Vipera aspis*, *Vipera latastei*, and *Vipera seoanei*. These species represent the totality of snakes present in Spain. Tables 3.1 and 3.2 summarize their main characteristics. Water dependence and water food dependence were rated between 0 and 3.

Table 3.1: Main characteristics of Spanish snakes (I)

Sources: Steward (1971); Blázquez and Pleguezuelos (2002); Gosá (2002); Pleguezuelos and Honrubia (2002); Brito (2004); Feriche (2004); Galán (2004); TIUCN (2004); Santos (2004); Santos and Pleguezuelos (2004); Pleguezuelos (2005)

Species	Spanish common name	English common name	Endemic	IUCN Category	Spanish Category	Deciduous Forest	Coniferous Forest	Shrubs	Low vegetation	Aquatic	Urban
<i>Coronella austriaca</i>	Culebra lisa europea	Smooth Snake	No	NE	LC	+	-	+	+	-	-
<i>Coronella girondica</i>	Culebra lisa meridional	Southern Smooth Snake	No	NE	LC	+	+	+	+	-	-
<i>Hemorrhois hippocrepis</i>	Culebra de herradura	Horseshoe snake	No	NE	LC	+	+	+	+	-	+
<i>Coluber viridiflavus</i>	Culebra verdiamarilla	European whip snake	No	NE	LC	-	-	+	+	-	-
<i>Elaphe longissima</i>	Culebar de esculapio	Aesculapian snake	No	NE	DD	+	+	+	+	-	-
<i>Elaphe scalaris</i>	Culebar de escalera	Ladder snake	Yes	NE	LC	-	-	-	-	-	-
<i>Macroprotodon brevis</i>	Culebra de cogulla	Hooded snake	No	NE	NT	+	+	+	+	-	-
<i>Malpolon monspessulanus</i>	Culebra bastarda	Montpellier snake	No	NE	LC	+	+	+	+	-	-
<i>Natrix maura</i>	Culebra viperina	Viperine snake	No	NE	NT	-	-	-	-	+	-
<i>Natrix natrix</i>	Culebra de collar	Ringed snake	No	NE	NT	+	-	+	+	+	-
<i>Vipera aspis</i>	Víbora aspid	Asp viper	No	NE	LC	+	+	+	+	-	-
<i>Vipera latastei</i>	Víbora hociCUDA	Snub-nosed viper	No	NE	NT	+	+	+	+	-	-
<i>Vipera seoanei</i>	Víbora de Seoane	Seoane's viper	Yes	NE	LC	+	-	+	+	-	-

NE=Not Evaluated; NT=Near Threatened; DD=Data Deficient; LC=Least Concern.

+ =Presence; - =Absence.

Table 3.2: Main characteristics of Spanish snakes (II)

Species	Elevation Range (m)	Preferred Annual Precipitation (mm)	Preferred mean annual temperature (°C)	D/N/C	Reproduction	Body size (mm)	Water dependence	Dependence of diet on water	Hibernation	Main Threats
<i>Coronella austriaca</i>	0-2700	>600-800	No data	D	Ovoviviparous	700	1	1	+	Forest fires, habitat alteration
<i>Coronella girondica</i>	0-2150	No data	No data	C/N	Oviparous	600	0	1	+/-	Run over. Habitat alteration
<i>Hemorrhois hippocrepis</i>	0-1750	170-1800	12.0-18.5	D	Oviparous	1500	0	1	+/-	Direct extermination
<i>Coluber viridiflavus</i>	70-2000	No data	No data	D	Oviparous	1200	1	1	+	Run over
<i>Elaphe longissima</i>	60-1200	>700	No data	D	Oviparous	1100	1	1	+	Direct extermination Run over
<i>Elaphe scalaris</i>	0-2200	170-2000	>10°	N / D	Oviparous	1100	0	1	+	Run over. Habitat alteration
<i>Macroprotodon brevis</i>	0-1500	170-2000	> 12°C	C/N	Oviparous	450	0	1	+/-	Habitat alteration
<i>Malpolon monspessulanus</i>	0-2100	170-2000	10-18.5	D	Oviparous	1800	1	1	+	Direct extermination Run over
<i>Natrix maura</i>	0-1500	No data	No data	D	Oviparous	750	3	3	+/-	Water pollution, run over, direct extermination
<i>Natrix natrix</i>	0-3060	No data	No data	D	Oviparous	800	3	3	+/-	Water pollution, run over, direct extermination
<i>Vipera aspis</i>	0-2500	No data	No data	D	Ovoviviparous	600	0	1	+	Habitat alteration Direct extermination
<i>Vipera latastei</i>	0-3000	No data	No data	D	Ovoviviparous	550	0	1	+	Direct extermination, forest fires, run over
<i>Vipera seoanei</i>	0-1900	No data	No data	D	Ovoviviparous	450	1	1	+	Habitat alteration, forest fires

D=Diurnal; N=Nocturnal; C=Crepuscular.

+ = The species hibernates in all its geographic range.

+/- = The most meridional populations are active the whole year.

According to this rating scheme a species completely independent of water would be rated with a zero and a species entirely dependent on water for living (reproduction, diet, etc.) was assigned a rating of 3. Along the same lines, in the “dependence of diet on water” column, a species that hunts prey independent of water (such as some birds or insects) were rated zero and species hunting aquatic prey (amphibians or fish) were rated with a three.

Tragsa (2002: 3) claims that the instructions given to the herpetologists responsible for sampling the cells were that “each cell had to be entirely sampled as well as all the habitats included in them”. Tragsa also add that “each habitat had to be sampled at least on two occasions during the most favourable activity period for the herpetofauna”. Furthermore, for each habitat, the efforts taken to locate herpetofauna had to be equivalent.

The number of reptile and amphibian sightings in individual cells differs substantially across Spain. It is not known for certain how much of this difference is due to the actual abundance of reptiles and amphibians and how much may be related to how often the areas have been surveyed. The number of cells in which species were missed but in which they were actually present (false negatives) cannot be estimated, but I believe that the absence data at the individual species level, while not perfect, is good.

Figure 3.6 shows the number of times herpetofauna have been recorded as present across the Spanish Iberian Peninsula for 10 x 10 km areas, referenced to UTM coordinates, according to the “*Atlas y Libro Rojo de los Anfibios y Reptiles de España*” (Pleguezuelos et al., 2002).

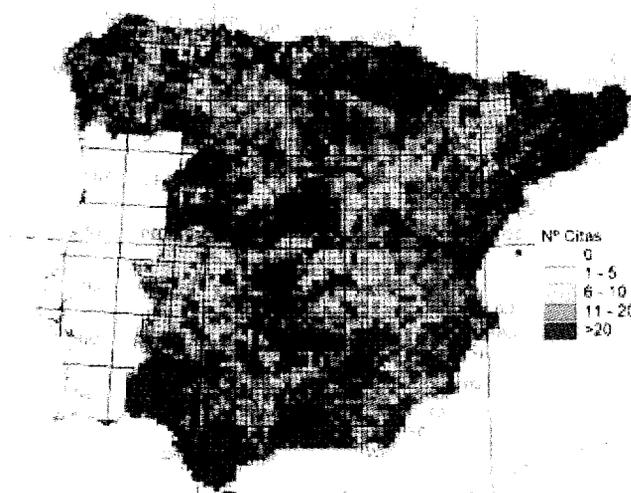


Figure 3.6: Density of reporting sightings in individual cells including all the species of amphibians and reptiles in the Spanish Iberian Peninsula. Source Pérez-Mellado (2002).

Because maps included in the atlas do not exactly follow the coastline, coastal cells were truncated in order to follow the real shorelines as closely as possible. However, following the Hawkins and Porter (2003a, 2003b) procedures, adjacent truncated coastal cells were often combined to obtain areas approximately equal in size to inland cells. A species was considered present in a cell if any part of its range overlapped the cell.

The study area was defined as “the spatial extent chosen within which the study is conducted” (Morrison and Hall (2002: 52). The extent of the study area defines the scale of analysis. Consequently, the study area was the Spanish Iberian Peninsula while the scale of analysis was delimited by the political and physical boundaries of the Spanish Iberian Peninsula. Within the study area, resolution was defined as “the smallest spatial scale at which we portray discontinuities in biotic and abiotic factors in map form” (Hargis et al., 1997; see Morrison and Hall, 2002: 52). This research was conducted in a 10 x 10 km resolution in UTM referenced cells (Figure 3.7).

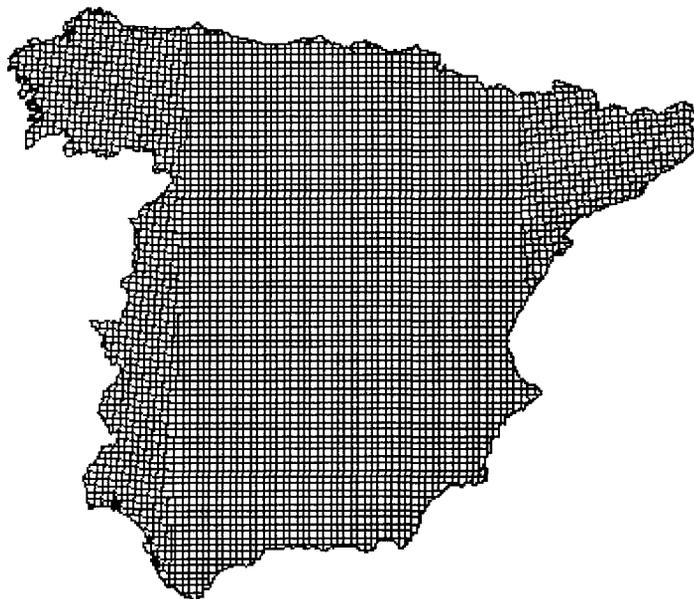


Figure 3.7: Four thousand nine hundred and forty five standard grid cells with a 10 x 10 km resolution. West and east portions correspond to the 29 and 31 UTM zones, respectively. These areas do not seem straight because were referenced to the central UTM zone of Spain (30).

3.2 Assumptions of logistic regression

Logistic regression is a statistical technique that can be used for evaluate the relation of one or more independent variables with a binary dependent variable.

The theory of logistic regression and examples of the types of analysis to which it has been applied were discussed in Section 2.3.2. In this section, the conditions that must apply for it to be used, other complicating factors related to specific aspects of its use for model building, and its application to the situation under investigation will be discussed.

Logistic regression has no assumptions about the distribution of the predictors; the independent variables do not have to be normally distributed, nor linearly related, nor of equal variance within each group (Tabachnick, 2000). The only requirements are that the observations must be independent and that the variables must be linearly related to the log of the odds that an event occurs (logit) (Norusis, 2003).

3.2.1 Linearity

In the logistic regression model, the relationship between the logit and the values of an independent variable must be linear. This assumption is not easy to check in logistic regression (Norusis, 2003) but several graphical and statistical methods are available. The procedure described by Norusis (2003: 342) has been chosen because, as she states, “it is one of the simplest techniques to assess linearity in logistic regression”.

According to this method, each continuous variable is transformed into a categorical variable. Each category is built in a manner that generates intervals of equal width so that the expected relationship between the coefficients of the categorical variable and the categories are linear. These coefficients correspond to the β_i values in the logistic regression equation:

$$[3.1] \quad f(z) = \frac{1}{1 + e^{-(\alpha + \beta_i X_i)}}.$$

The logistic regression is then run with the grouping of the continuous variable as a categorical variable. If the relationship between the logit and the values of the predictor is linear, the coefficients of the categorical variable should increase or decrease more or less linearly.

The values of the coefficients were also plotted graphically to assess more easily the linearity of the coefficients, although care must be taken to ensure that all categories are plotted. When a variable is defined as “categorized” in SPSS, the procedure generates as many contrast analyses as the number of categories minus one. Each contrast analysis gives a coefficient for each category of the variable except for the omitted one. The latter is called the reference category because the contrast analysis is done comparing each

category with the reference one. Finally, the omitted category has a coefficient of zero; Norusis (2003) states that it must also be placed in the plot.

As will be discussed in section 4.3, those variables that are “Not linear” were not included in the subsequent analyses. Those variables that were called “Half linear” were introduced in the analysis but always taking into account the fact that the linearity presumption was not perfectly fulfilled. “Half linear” was established when three points of the plot essentially followed a line but the fourth one showed some degree of deviation.

3.2.2 Independence of the observations: Spatial Autocorrelation (SA)

Environmental variables are frequently spatially autocorrelated such that sites in close proximity are more similar than sites separated by greater distances (Knapp et al., 2003). Therefore, the premise of independence of the observations often is not fulfilled. Although long known by statisticians as a source of problems SA has been ignored by geographical ecologists until recent years (Lennon, 2000). Depending on purpose the fact that observations are autocorrelated may or may not be important. There is the view that autocorrelated data is fundamental to pattern. The effect of this is of course that confidence limits are inflated. Because of this I have chosen to adjust the protocol and ignore tests of inference.

In classical statistical testing, one counts one degree of freedom for each independent observation. However, with autocorrelated data, because of the lack of independence, new observations do not each bring with them one degree of freedom (Legendre, 2003). The consequence is that the probability of a Type I error is often

under-estimated. Hence, some results are declared to be significant when in truth there is not such significance.

Moran's I was applied to measure the overall pattern of dependence present in the environmental variables. This is the most commonly used index in univariate autocorrelation analyses (Diniz-Filho et al., 2003). It varies between -1.0 and 1.0 for maximum negative and positive autocorrelation, respectively. Positive values imply that nearby areas tend to be similar in attributes; negative values, dissimilar; and zero values denote uncorrelated, independent, and random arrangement of attribute values (Lo and Yeung, 2002).

The first step in the analysis of SA is to construct a spatial weights matrix containing information on the "neighbourhood" structure for the studied grid (Anselin, 2003). Different criteria can be used to measure contiguity between cells. In the current research, the queen-based contiguity index was used because it measures the maximum number of neighbourhood surrounding each cell. As shown in Figure 3.8, the queen criterion determines neighbouring units as those that have any point in common, including common boundaries and common corners (Anselin, 2005).

Subsequently, Moran's I was measured for different orders of contiguity. Plotting these values against the different orders of contiguity allowed evaluating the behaviour of autocorrelation as a function of spatial distance, in a graph called spatial correlogram (Diniz-Filho et al., 2003). In this case, the correlograms as a whole can be considered significant at a given significance level α if at least one of its coefficients is significant at α/k , where k is the number of contiguity classes used (Bonferroni criterion) (Oden, 1984 *see* Diniz-Filho et al., 2003).

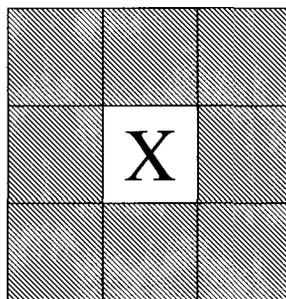


Figure 3.8: Diagram showing the queen-based contiguity criterion of an observation **X**. This criterion determines neighbouring cells as those that have any point in common, including both common boundaries and corners.

The primary interest of the current research when developing the models was to identify strong predictors of snakes' distributions rather than identifying all factors that may show a statistical association with the patterns of distributions. Hence, minor variables likely to be influenced by spatial autocorrelation were not interpreted (Hawkins and Porter, 2003). Because spatial autocorrelation in the data was found, significance levels from regressions are probably greater than is justified. However, the coefficient of determination is not calculated based on the degrees of freedom of the sample, so it is not affected by spatial autocorrelation. As a result, the models that were used in this study were based on the coefficient of determination and not on the significance of the variables (Diniz-Filho et al., 2003). Consequently, to find associations with ecological significance, that is, strong predictors, at each step of the stepwise selection I evaluated each variable based on the coefficient of determination and stopped when the addition of a variable did not improve the model R^2 by at least 5% (Rodriguez et al., 2005). This means that biological more than statistical criteria were taken into account as the basis to develop the models.

3.3 Model building process

The species distribution models were developed by relating recent environmental maps (climatic and topographical) to the species distribution. The resultant models were used to project the species presence/absence in each cell for the Hadley climate scenario for 2020. This projection was accomplished by substituting the contemporary values of the predictor variables for those of Hadley 2020 scenario, and then applying the species models to calculate the potential new distributions.

Figure 3.9 summarizes the steps that were followed to develop the species projections.

3.3.1 Species filtering

The selection of the snake species for which projections are conducted was based on the strength of the correlation of their current distribution with the available environmental variables. Those species whose distributions show weak correlations with the environmental variables were not introduced into the analysis because the models produced would not be reliable. A coefficient of determination value of 0.4 was established as the minimum threshold for application of the model to project the future distribution of a species.

3.3.2 Model calibration

This step encompasses the estimation and adjustment of the model parameters and constants to the data and, as Guisan and Zimmermann (2000: 166) indicated, is “the more

global phase of model construction, which includes the selection of explanatory variables”.

Therefore, before data analysis was conducted, correlation coefficients for all pairwise combinations of independent variables were calculated. Because skewed data were found, it was decided to use the Spearman’s rank correlation coefficient. A significant value of $|r_s| \geq 0.85$ would indicate collinearity between two variables (Knapp et al., 2003).

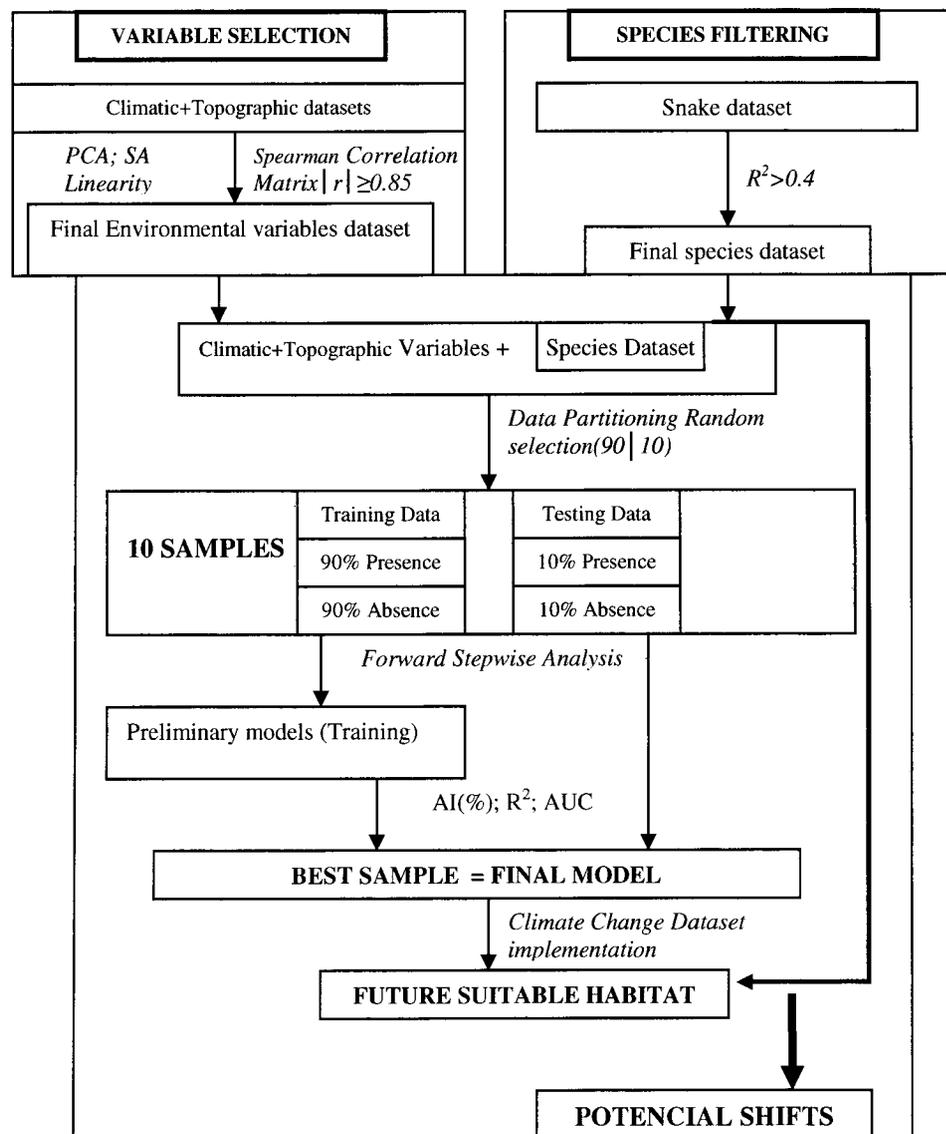


Figure 3.9: Overview of the model development phase

Based on biological criteria, the less important of the two variables was rejected. For example, Altwegg et al. (2005) found that winter temperature affected the survival of *Vipera aspis* juveniles because young individuals might be likely to run out of fat reserves during hibernation. In my data, the correlation between minimum winter temperature and annual temperature has a significant value of 0.89. Therefore, when both variables entered into the *Vipera aspis* models, annual temperature would be dropped. However, the simplicity of the models, made possible that the biological criteria was only applied in the model calibration of one species (see section 4.3 for further details).

Principal Component Analysis (*PCA*) (Varimax Rotation) was run in an attempt to better understand from an ecological perspective the predictors and to find underlying patterns and associations between them. Principal Component Analysis (*PCA*) is a technique that is widely used to simplify a dataset (e.g. Atauri and Lucio, 2000), or more formally, it is a linear transformation that selects a new coordinate system for the data set such that the greatest variation by any projection of the data set comes to lie on the first axis (called principal component), the second greatest variance on the second axis, and so on (Jolliffe, 1986).

In logistic regression, forward stepwise selection was chosen for this study because it has shown better predictive abilities and more stable models than backward selection (Berg, 2004). According to this procedure, variables are added to a model one at a time. The automated procedure starts out with a model that contains only the constant. At each step, the variables that enter into the model are the ones that have the smallest observed significance level for the score statistic (Norusis, 2003), or that have the highest correlation with the response scores (Zellner et al., 2004). At each step, the variables in

the remaining set are considered for inclusion in the current model. Forward selection continues until the stopping rule is satisfied (Zellner et al., 2004). The stopping rule chosen was a maximum number of iterations equal to 20. In addition, the criterion for inclusion of each variable at each step in the model was a probability value equal to 0.05. The score statistic used was the *RAO* statistic (Hoshmer and Lemeshow, 2000). These are all conventional values and SPSS defaults.

3.3.3 Model validation

Any approach to ecological modelling has little merit if the predictions are not assessed for their accuracy using independent data (Verbyla & Litaitis, 1989). As a very large data set formed the basis of this study, a quasi-independent data set for evaluation, obtained by randomly splitting the original dataset could be used. Nevertheless, as both data sets still covered the same study area, the data sets could not be considered as fully independent. In this respect, Chatfield (1995) questioned the use of data partitioning for model testing, suggesting that splitting data arbitrarily is not the same as collecting new data. A fully independent data set should also cover a distinct geographical area. Hence, as Guisan and Hofer (2003) indicated, they should preferably be identified as quasi-independent datasets.

The method of data partitioning used in this study has been termed the “*split-sample approach*” (Guisan and Zimmermann, 2000) or “*a $k=2$ cross-validation*”, (Fielding and Bell, 1997) where data are randomly split into two sets, one learning (or training) and one validation (or testing).

A trade-off between the learning and validation test sizes had to be taken into account. In the current research priority was given to the training dataset by selecting a large sample to build the model (90 % of the data) in order to obtain better model accuracies (Fielding and Bell, 1997). Therefore, a resampling method was carried out. Data were divided into a training dataset, corresponding to a random sample of 90% of the presence and 90% of the absence points; and a testing dataset with the remaining points (10 % presence and 10 % absence). This sampling process was selected, instead of splitting the population directly into a 90% learning random sample and a 10% validating random sample in order to reflect the same proportion of presence/absence in each learning/validation sample as in the total population. If the latter is not done, the estimated coefficient of the constant would be incorrectly calculated (Norusis, 2003). This process was replicated ten times for each species.

Finally, the best model among the ten replications was chosen to implement the climate change variables and produce the future distribution of the species and the amount of change maps.

3.3.3.1 Accuracy Index in percent (AI (%))

When measuring the association between predicted and observed values, the outputs of the models need to be transformed back to the scale of the real observations. The general rule is to use a 0.5 cutpoint (e.g. Berg et al., 2004; Cowley et al., 2000). Therefore, when predicted probabilities were higher than 0.5, they corresponded with observed occurrences and when values were lower than 0.5, with absences. Overall accuracy was defined as:

$$[3.2] \quad AI(\%) = \frac{n - (FN + FP)}{n} * 100$$

This is an accuracy index in percent, where *FN* and *FP* represent the number of False Negatives (i.e. omissions) and False Positives (i.e. commissions) respectively and *n* is the total number of testing cells. The goal of *AI*(%) is to count all errors against the correct number of presences and absences to be detected (Pouliot et al., 2002).

3.3.4 Model discrimination

Model discrimination evaluates the ability of the model to distinguish between presence and absence, based on the estimated probability of the event occurring.

The area under the *ROC* (Receiver Operating Characteristic) curve provides a measure of the model's ability to discriminate between those cells that produce presence versus those that produce absence. Hence, this type of curve has been used as a measure of discrimination. This curve, originating from signal detection theory, shows how the receiver discriminates the existence of signal in the presence of noise. It plots the probability of detecting true signal (sensitivity) and false signal (1-specificity) for an entire range of possible cutpoints (Hosmer and Lemeshow, 2000). Sensitivity (true positives) and specificity (true negatives) measure the proportion of sites at which the observations and predictions agree (Pearce and Ferrier, 2000):

$$[3.3] \quad \text{Sensitivity} = \frac{\text{Number of positive sites correctly predicted}}{\text{Total number of positive sites in the sample}}$$

$$[3.4] \quad \text{Specificity} = \frac{\text{Number of negative sites correctly predicted}}{\text{Total number of negative sites in the sample}}$$

A plot of sensitivity versus 1-specificity over all possible cutpoints (Figure 3.10) is called the “*ROC* curve” and the area under the curve (*AUC*) provides a measure of

discrimination between presence and absence of species (Hosmer and Lemeshow, 2000). The value of the *AUC* is constrained to be between 0.5 and 1.0. If the value is 0.5, the scores for the presence or absence do not differ, while a value of 1.0 indicates no overlap in the distributions of presences and absences. *AUC* is very useful as the criterion for selection among different classifiers because it avoids the problems associated with threshold effects found in most error measures (Fielding and Bell, 1997).

As a general rule, Hosmer & Lemeshow (2000) indicate that:

If $ROC = 0.5$: this suggests no discrimination.

If $0.7 \leq ROC \leq 0.8$: this is considered acceptable discrimination

If $0.8 \leq ROC \leq 0.9$: this is considered excellent discrimination

If $ROC \geq 0.9$: this is considered outstanding discrimination.

However, as Hosmer and Lemeshow (2000) pointed out, model performance is not only a question of discrimination, it should be assessed on a combination of calibration and discrimination.

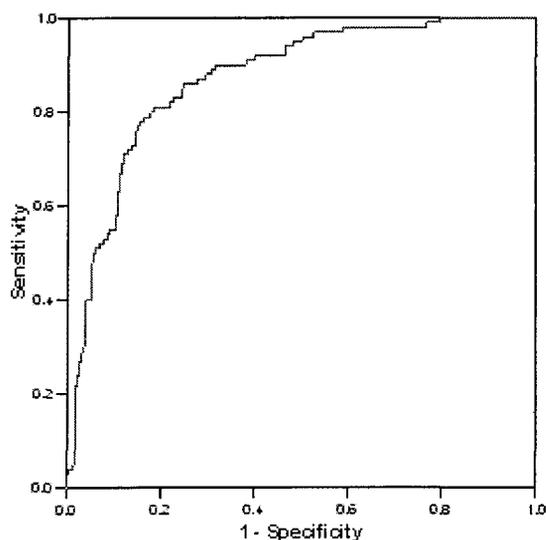


Figure 3.10: Plot of sensitivity versus 1-specificity for all possible cutpoints in the 10th replication sample of *Hemorrhoids hippocrepis*. $AUC = 0.871$

3.3.5 Selecting the best models

Model performance and best sample selection were evaluated based on the combination of three criteria: *AUC* (Fielding and Bell, 1997; Guisan and Hofer, 2003), coefficient of determination or R^2 (Dettmers et al., 1999) and *AI (%)* (Pouliot et al., 2002). For each species I ranked each sample giving a 10 to the maximum *AUC*, R^2 , and *AI (%)* value and counting down until 1. Because the three indices usually did not coincide for the same sample, an adjusted average was used to select the optimal sample model based on equation [3.5]. The value is termed the “Adjusted Weight Rank” (*AWR*).

$$[3.5] \quad AWR = \frac{0.5(AUC_Rank) + 1(R^2_Rank) + 1.5(AI(\%)_Rank)}{3}$$

AWR can vary between 1 and 10.

As Chatfield (1995; see Fielding and Bell, 1997: 38) indicated, “it is advantageous to adopt a pragmatic approach to model building in which the focus is on the model’s accuracy and usefulness, rather than its statistical validity”. In this respect, the accuracy of the models was considered as the most important selection criterion, followed by the R^2 and the area under *ROC* curve.

CHAPTER 4

RESULTS AND DISCUSSION

This chapter consists of three parts. The outputs derived from the analysis of climate and topography variables are firstly discussed. For this aim, a correlation matrix, principal components analysis, linearity and presence of spatial autocorrelation were examined.

Subsequently, the Spanish snakes are divided into two groups according to their potential to be modelled. Six snakes not amenable to be modelled comprised the first group while the second group was formed by those snakes for which the relation between the environmental variables and the snakes' distributions was strong enough to produce a reliable model.

Finally, each species modelled was presented as a series of four maps: current distribution map derived from the "*Atlas y Libro Rojo de Anfibios y Reptiles de España*" (Pleguezuelos et al., 2002); a map of the potential current distribution derived from the models; a map of the projected suitable habitat; and the potential distributional shifts. The credibility of these models was judged. Maps were then created to indicate a prioritization from a physiographic perspective for the species modelled.

4.1 Climate and Topographic variables

4.1.1 Correlation matrix

A Spearman correlation matrix was obtained to find redundant information between variables. The purpose was to identify pairwise correlated variables in order to allow one to be dropped during the model calibration phase.

As indicated in Table 4.1, there are high correlations between some variables. Furthermore, most correlations are highly significant but some show quite weak relationships. Two reasons are probably responsible for this result. First, the large number of observations makes it possible that all correlations are likely to be significant. Second, the spatial autocorrelation in the data has led to significance levels for the regressions that are probably greater than is justified (Lennon, 2000).

It was necessary to drop a variable because of correlation problems in only one logistic regression. This occurred for *Vipera aspis* for which maximum autumn temperature and minimum summer temperature entered as the second and third variables respectively in the stepwise selection. Models with both variables were tested and finally maximum autumn temperature was selected because produced a more parsimonious model.

4.1.2 Principal components analysis

The axes generated from this technique were not incorporated directly into the models as a replacement of the original variables because it would have resulted in loss of information pertaining to the real weight of each variable affecting the species. Instead, Principal Component Analysis was run in an attempt to better understand the predictors and to find underlying patterns and associations between them.

After a Varimax transformation of the principal components was conducted maximising their correspondence to the original variables, three axes produced

Table 4.1: Pairwise correlation matrix between each of the environmental variables used in the current research

		AnnT	MaxsprT	MaxsumT	MaxautT	MaxwinT	MinsprT	MinsumT	MinauT	MinwinT	AnnP	SprP	SumP	AutP	WinP	TRange	Elev	ElevRang
MaxsprT	<i>r</i>	0.97																
	<i>Sig.</i>	0.00																
MaxsumT	<i>r</i>	0.81	0.89															
	<i>Sig.</i>	0.00	0.00															
MaxautT	<i>r</i>	0.98	0.99	0.88														
	<i>Sig.</i>	0.00	0.00	0.00														
MaxwinT	<i>r</i>	0.95	0.88	0.65	0.92													
	<i>Sig.</i>	0.00	0.00	0.00	0.00													
MinsprT	<i>r</i>	0.97	0.90	0.67	0.91	0.96												
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00												
MinsumT	<i>r</i>	0.98	0.95	0.80	0.95	0.90	0.95											
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00											
MinauT	<i>r</i>	0.97	0.90	0.66	0.91	0.96	0.99	0.95										
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00										
MinwinT	<i>r</i>	0.89	0.78	0.50	0.81	0.94	0.96	0.84	0.96									
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00									
Annual P	<i>r</i>	-0.39	-0.47	-0.53	-0.44	-0.25	-0.28	-0.43	-0.27	-0.13								
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00								
Spring P	<i>r</i>	-0.73	-0.76	-0.73	-0.76	-0.62	-0.62	-0.72	-0.62	-0.50	0.83							
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00							
SummerP	<i>r</i>	-0.73	-0.76	-0.84	-0.80	-0.61	-0.60	-0.69	-0.60	-0.48	0.57	0.83						
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
Autumn P	<i>r</i>	-0.16	-0.25	-0.32	-0.20	-0.02	-0.07	-0.23	-0.06	0.08	0.93	0.61	0.31					
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
Winter P	<i>r</i>	-0.17	-0.27	-0.31	-0.20	-0.02	-0.08	-0.25	-0.07	0.08	0.91	0.60	0.27	0.98				
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
TRange	<i>r</i>	0.17	0.33	0.68	0.30	-0.02	-0.03	0.19	-0.04	-0.23	-0.40	-0.31	-0.46	-0.35	-0.34			
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.14	0.03	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00			
Elev	<i>r</i>	-0.80	-0.75	-0.43	-0.72	-0.83	-0.88	-0.77	-0.87	-0.89	0.13	0.41	0.31	-0.03	0.01	0.20		
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.36	0.00		
ElevRang	<i>r</i>	-0.32	-0.40	-0.43	-0.36	-0.21	-0.26	-0.30	-0.23	-0.17	0.53	0.50	0.43	0.42	0.45	-0.31	0.31	
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Slope	<i>r</i>	-0.34	-0.43	-0.45	-0.38	-0.22	-0.28	-0.33	-0.26	-0.18	0.56	0.53	0.44	0.46	0.48	-0.32	0.32	0.97
	<i>Sig.</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

r = Spearman Coefficient. A $|r| \geq 0.85$ that has been demonstrated to be statistically significant would indicate redundancy between two variables (Knapp et al., 2003). Sig = Significance level. Variables showing redundant information according to the current research are bold.

eigenvalues ≥ 1 and together explained 91 % of the variance of the original data (Table 4.2). The remaining axes were assumed to be noise because they showed eigenvalues < 1 and were discarded from the analysis (Badgley and Fox, 2000).

Table 4.2: Total variance explained by the first three components of the PCA

Component	Initial Eigenvalues			Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	11.011	61.175	61.175	8.868	49.266	49.266
2	4.189	23.270	84.445	5.490	30.499	79.764
3	1.293	7.184	91.628	2.136	11.864	91.628

The first axis contains 61 % of the variance. The loadings presented in Table 4.3 indicate that this axis is dominated by annual temperature and the minimum and maximum seasonal temperatures with high positive loadings and by elevation that has negative loading. The inclusion of elevation in this component is probably a consequence of the atmospheric lapse rate, which is the decrease in measured air temperature with increasing altitude. Temperature usually decreases with elevation by about 6.4°C/1000 m (Strahler and Strahler, 2005).

The second axis explains 23 % of the variance and depicts a precipitation-temperature relationship gradient. In this axis, annual and maximum and minimum precipitation have high positive loadings and temperature range and maximum summer temperature have high negative loadings (Table 4.3). This temperature association for this axis is probably the expression of the role of water in temperature regulation. The high specific heat of water means that its presence strongly influences the amount of energy required to change the temperature of an object (Strahler and Strahler, 2005). It requires large amounts of heat energy to raise its temperature and large amount of heat

energy are released as it cools. Water's high specific heat allows for the moderation of local and regional temperatures. For example, the north-western region of Spain, where rainfall is more abundant, tends to have fewer abrupt changes in temperature; the temperature changes are moderated by precipitation. In addition, higher precipitation rates allow the development of more complete and taller vegetation covers that also moderate the climate.

Table 4.3: Loadings of the rotated component matrix (Varimax rotation). Cells are shaded according to the component where the variable was included.

	Component		
	1	2	3
Minimum Autumn Temperature	0.980	-0.077	-0.127
Minimum Spring Temperature	0.978	-0.079	-0.152
Maximum Winter Temperature	0.970	-0.060	-0.094
Minimum Winter Temperature	0.963	0.128	-0.157
Annual Temperature	0.953	-0.264	-0.131
Minimum Summer Temperature	0.913	-0.330	-0.096
Maximum Autumn Temperature	0.911	-0.358	-0.110
Maximum Spring Temperature	0.884	-0.389	-0.159
Maximum Summer Temperature	0.613	-0.703	-0.054
Elevation	-0.859	-0.142	0.372
Winter Precipitation	-0.007	0.906	0.206
Autumn Precipitation	-0.020	0.881	0.255
Temperature Range	-0.139	-0.853	0.071
Annual Precipitation	-0.202	0.913	0.256
Summer Precipitation	-0.462	0.708	0.204
Spring Precipitation	-0.472	0.783	0.268
Elevation Range	-0.229	0.304	0.894
Slope	-0.261	0.349	0.876

The third axis explains 7 % of the variance. The loadings indicate this axis is dominated by elevation range and slope, both with high positive values. It is expressing the effect of a topographic gradient according to which, for those zones where the elevation range is greater, the slopes tend to be steeper.

In conclusion, three basic axes were obtained that were labelled: temperature-elevation, precipitation-temperature range and topography. The Iberian Spanish Peninsula, where this study was conducted, and the variables used confirmed general

theories of physical geography such as lapse rate or the role of water in regulating climate. Furthermore, no unexpected patterns emerged from the *PCA*.

4.1.3 Linearity

Kahane (2001) pointed out that a decrease in model performance is the main consequence of not accounting for linearity when models are calibrated. Linearity was analyzed following the procedure proposed by Norusis (2003) (see section 3.2.1). The procedure for assessing linearity will be illustrated by the example of annual temperature, as related to *Hemorrhoids hippocrepis*.

Annual temperature, a continuous variable, was categorized into four different intervals of equal width. Four intervals also were applied to all other variables used in the analyses. Although Norusis (2003) suggests using three categories: low, normal and high, an extra category was added in the current research because an extra point allows easier visual assessment of linearity in the plots. Stepwise logistic regression analysis was then run using the presence/absence of *Hemorrhoids hippocrepis* as dependent variable and categorizing annual temperature as the predictor. When a variable is defined as “categorized” in SPSS, the procedure generates as many contrast analyses as the number of categories minus one. Each contrast analysis gives a coefficient for every category of the variable except for the omitted one. The latter is called the reference category because the contrast analysis is done comparing each category with it. SPSS allows choosing between the first and the last categories to be the reference one. In this example the last category was the reference category. The omitted value will need to be replaced with a zero as described by Norusis (2003)

In Table 4.4, the β_i values correspond to the coefficients in the logit equation:

$$\alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3.$$

Table 4.4: Logistic regression coefficients (β_i) when annual temperature as a categorical variable is related to *Hemorrhoids hippocrepi* presence/absence

	β_i
Annual temperature 1 st Category	6.15
Annual temperature 2 nd Category	4.77
Annual temperature 3 rd Category	3.15

When the logistic regression coefficients are plotted against their categories (Figure 4.1), the linearity of the variable is confirmed meaning that this variable fulfils the logistic regression linear assumption.

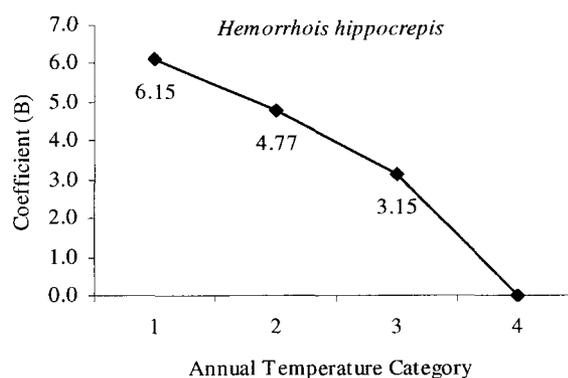


Figure 4.1: Linearity plot of annual temperature when assessed against *Hemorrhoids hippocrepi*.

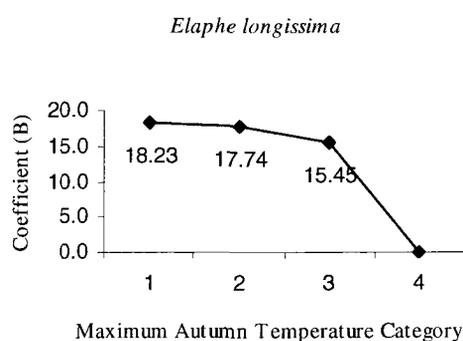
Table 4.5 shows the results of the linearity analyses of the independent variables against the presence/absence data for each species. In these analyses, “Not linear” was established when the variables were clearly not linear. A variable was declared “Half linear” when the relation was not linear in total but when three points of the plot

Table 4.5: Summary of the linearity assessment for each variable when they were analyzed against the presence/absence of each species

	<i>Coluber viridiflavus</i>	<i>Coronella austriaca</i>	<i>Elaphe longissima</i>	<i>Hemorrhois hippocrepis</i>	<i>Macroprotodon brevis</i>	<i>Vipera aspis</i>	<i>Vipera seoanei</i>
Ann.T	Linear	Linear	Linear	Half linear	Linear	Linear	Linear
Max.Spr.T	Linear	Half linear	Linear	Half linear	Linear	Linear	Linear
Max.Sum.T	Linear	Half linear	Linear	Half linear	Linear	Linear	Half linear
Max.Aut.T	Linear	Half linear	Linear	Linear	Linear	Linear	Half linear
Max.Win.T	Linear	Half linear	Half linear	Half linear	Linear	Half linear	Half linear
Min.Spr.T	Linear	Linear	Linear	Linear	Linear	Linear	Half linear
Min.Sum.T	Linear	Linear	Linear	Half linear	Linear	Linear	Linear
Min.Aut.T	Linear	Linear	Linear	Half linear	Linear	Linear	Half linear
Min.Win.T	Linear	Linear	Linear	Not linear	Linear	Linear	Not linear
Ann.P	Linear	Half linear	Linear	Linear	Not linear	Half Linear	Linear
Spr.P	Linear	Half linear	Linear	Linear	Linear	Linear	Linear
Sum.P	Linear	Half linear	Linear	Half linear	Half linear	Linear	Linear
Aut.P	Not linear	Half linear	Linear	Linear	Not linear	Not linear	Linear
Win.P	Not linear	Half linear	Linear	Linear	Not linear	Not linear	Linear
T.Range	Not linear	Not linear	Linear	Linear	Not linear	Not linear	Linear
Elevation	Linear	Linear	Half linear	Not linear	Half linear	Linear	Not linear
Elev.Range	Not linear	Linear	Linear	Not linear	Not linear	Linear	Not linear
Slope	Not linear	Linear	Linear	Linear	Not linear	Linear	Linear

essentially followed a line but the fourth one showed some degree of deviation. Figure 4.2 presents graphical examples of what were considered “Not linear” and “Half linear”.

(a) Half linear



(b) Not linear

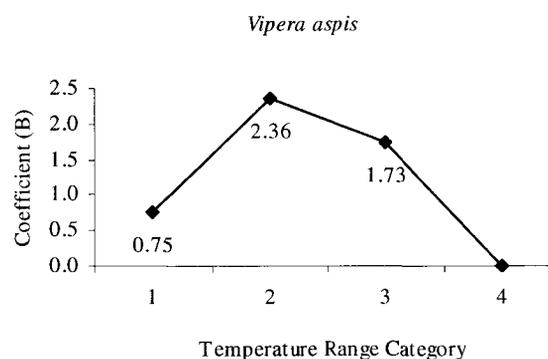


Figure 4.2: Example of half and not linear (a) Half linear: linearity plot of maximum autumn temperature when assessed against presence/absence *Elaphe longissima*. Not linear (b): linearity plot of temperature range when assessed against presence/absence *Vipera aspis*

“Not linear” variables were included in the analysis but none of them showed strong relationships with the species, that is, none of them entered into the models as main predictors. Furthermore, during the model building process for *Hemorrhoids hippocrepis*, elevation entered as the second most important variable, following maximum winter temperature. Elevation is not linearly related to the presence/absence of *Hemorrhoids hippocrepis*, and therefore it was decided to drop it for the purpose of model building and run the analysis without this variable. When this was done, summer precipitation entered as the second most important variable. It is argued that the implications of not including non-linear variables in model building were not highly influential for the final result, because the main variable governing the species distribution and explaining most of the variance was maximum winter temperature and not summer precipitation nor elevation. In addition, the decrease of the model's R^2 when using summer precipitation instead of elevation was very low (0.026 R^2 decrease for the selected replication).

Half linear variables were used in the analysis but always with recognition that the linearity assumption was not perfectly fulfilled and, hence, that those models that included half linear variables were probably less reliable than those using strictly linear variables (Kahane, 2001).

4.1.4 Spatial autocorrelation

The aim of this section is to assess if spatial autocorrelation exists in the dataset and needs to be addressed in the model building process.

The environmental variables used in this study were found to be patterned in space. The spatial correlograms in Figure 4.3 indicate that variables are positively autocorrelated. Although only six variables are presented, the same pattern was found for the remaining 12 variables. There is a general tendency towards a continuous decrease in Moran's I coefficients as the orders of contiguity increase. The greater is the distance between measurements, the weaker will be the dependency between them. This type of correlogram when SA is stronger at short distances and then decreases indicates that spatial variation is structured in patches. The distance up to which SA is observed has been interpreted as the average patch size in the variable (Diniz-Filho et al., 2003).

Figure 4.3 indicates that all variables presented strong spatial structure in the first orders of contiguity and then the slope of the curve tended to decrease as the orders of contiguity increased. Topographic variables showed a more patchy spatial structure for distances up to 10 to 15 orders of contiguity followed by Moran's I close to zero, beyond this distance (Figures 4.3 e,f). The topographic variables possessed a relatively low level of spatial structure (Diniz-Filho et al., 2003). Results also indicate that minimum summer temperature, maximum winter temperature and summer precipitation showed strong spatial autocorrelation patterns, with similar correlogram profiles (Figures 4.3 a,b,c): positive Moran's I for the whole plot where patch size limits exceed the distance limit considered for these correlograms. Strong mid-distance autocorrelation coefficients were observed for winter precipitation up to 20 orders of contiguity. After this distance Moran's I was close to zero. This means that this variable possesses a mid-level spatial structure, with patches larger than those shown for topographic factors, but smaller than the temperature variables.

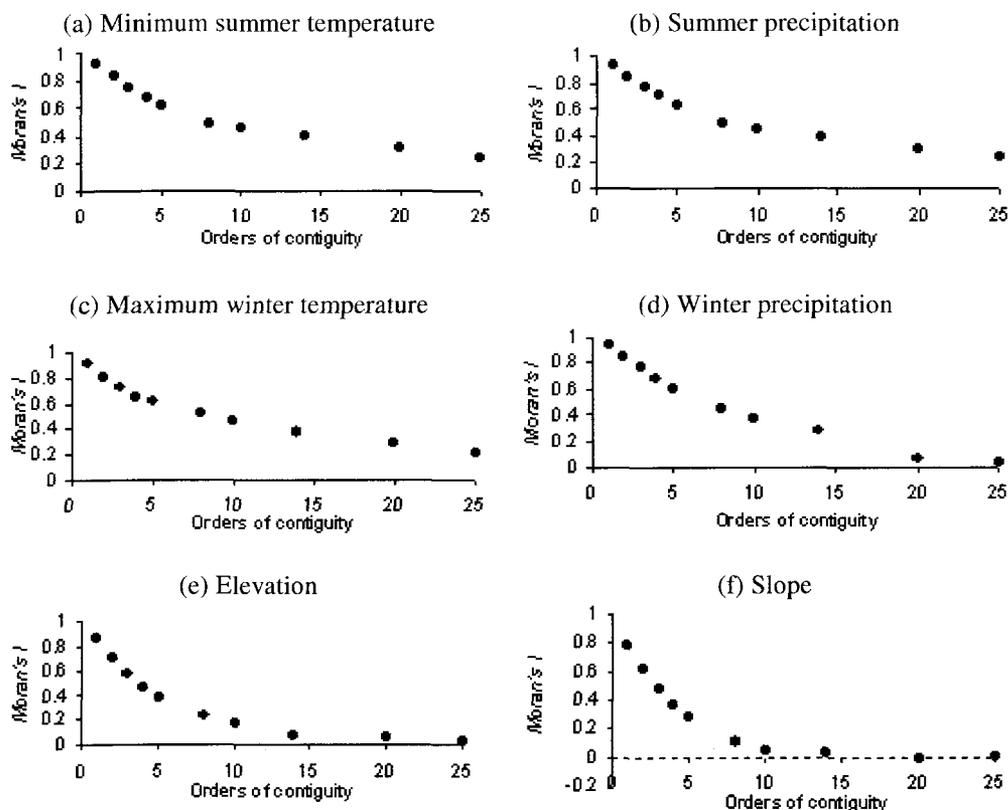


Figure 4.3: Spatial correlograms for (a) Minimum summer temperature; (b) Summer precipitation; (c) Maximum winter temperature; (d) Winter precipitation; (e) Elevation; (f) Slope. All correlograms are significant after Bonferroni correction.

When *SA* has been demonstrated to be present in data, several solutions are open to ecologists. In this research, a first attempt was carried out by removing samples in order to decrease possible spatial dependence. However, as stated by Legendre (1993) this solution is never recommended because it entails a net loss of important information. Instead, the whole dataset was used but the reliability of models was judged by the coefficient of determination. Because R^2 is not calculated based on the degrees of freedom of the sample, it is not affected by spatial autocorrelation (Diniz-Filho et al., 2003).

In this respect, in automated forward-stepwise selection, the variable with the smallest observed significance level for the score statistic is entered into the model at

each step (Norusis, 2003). Because spatial autocorrelation in the data has been shown to affect significance level, automatic procedures for variable entry into the models might not be adequate. Instead, Diniz-Filho et al. (2003) suggest the use of a manual iterative forward-stepwise selection procedure (Philippi, 1993). This procedure allows the user to set the decision for variable entrance (i.e. R^2 improvement). Consequently, the dependent variable was first regressed on each independent variable separately to create the best single-variable model based on the R^2 . A two variable model was then created by adding each of the remaining variables one at a time to the single-variable model to determine which improved it. This procedure continued until no remaining variable improved the model R^2 by at least 5 % (Rodríguez et al. 2005). The models produced by manual and automated stepwise selection were compared in sample replications and results were found to be exactly the same. Because manual stepwise selection is an extremely time consuming procedure, it was decided to use the automated procedure instead.

4.2 Spanish snake groupings

A primary goal of biogeography is to understand how climate variation in time and space affects the geographic distribution of species. This goal is becoming increasingly important because of the need to evaluate the effects of climate change on natural populations. Despite its obvious importance, few studies have attempted to quantify the ecological consequences of climate on snakes (Guisan and Hofer, 2003). A main reason for the lack of studies on the distribution of snake species is because so many factors apart from temperature, precipitation or elevation may be involved that it is impossible for an individual scientist to acquire the data needed. Even if the data are

available, it is challenging to integrate them so that specific, testable predictions can be made (Peterson et al., 1993).

Consequently, the goal of this research is to address: How will the distribution of the various snake species in Spain be affected by future changes in climate? It is assumed that climate is (and will be) an essential factor in determining species geographical ranges and that temperature is (and will be) critical in the ectothermal animal biology of snakes (and consequently in their distribution). It is also assumed that the current distribution of snake species in Spain can provide information that will allow projections to be made. The research will not address biological causes to explain why a species might be more influenced for one variable than other. Such biological hypotheses might better be tested at a local scale by experimental manipulation of the species. Further research should be done in this respect (Dodd, 1993). The information from the current research is more suited to allowing the prioritization of sites from a physiographic (climatic and topographic) perspective if the climate change scenario proposed by climate modelling processes are realized. This might be a helpful tool for conservation planners in delineating areas that should be protected.

Attempts were made to produce a model for the thirteen Spanish snakes, but logistic regressions were able to be developed for the possible distribution of only seven snake species, five of which were governed dominantly by precipitation while two were governed by temperature. The discussion will first address how this differentiation between the snakes amenable to be modelled and the snakes not amenable to be modelled was accomplished.

4.2.1. Snakes not amenable to be modelled

The coefficient of determination (R^2) gives an indication of how well the response variable (the species presence/absence) is explained by the predictors. This index has been used to explore which of the thirteen Spanish snakes have the potential to be modelled on a basis of changing climate scenarios. To accomplish this task, logistic regressions were carried out between the species distributions and the environmental variables. These 18 environmental variables were entered simultaneously into the regression process instead of by stepwise introduction. Because higher coefficients of determination may produce more reliable models, a high R^2 threshold such as 0.4 was selected (Table 4.6) for a species to be amenable to be modelled.

Table 4.6: Coefficient of determination (R^2) for the thirteen Spanish snakes. $R^2 > 0.4$ was selected as the cutpoint to model the species.

	Species	R^2
Not Modelled Species	<i>Coronella girondica</i>	0.097
	<i>Natrix maura</i>	0.106
	<i>Natrix natrix</i>	0.155
	<i>Vipera latasti</i>	0.190
	<i>Elaphe scalaris</i>	0.195
	<i>Malpolon monspessulanus</i>	0.195
Modelled Species	<i>Coronella austriaca</i>	0.420
	<i>Macroprotodon brevis</i>	0.457
	<i>Hemorrhois hippocrepis</i>	0.515
	<i>Elaphe longissima</i>	0.620
	<i>Vipera aspis</i>	0.654
	<i>Coluber viridiflavus</i>	0.666
	<i>Vipera seoanei</i>	0.699

As shown in Table 4.6 the logistic regression approximation of the distribution pattern of six widely distributed species of snakes proved to be particularly poor. Such results have also been found in other habitat modelling studies (e.g. Stockwell and Peterson, 2002; Brotons et al., 2004). Guisan and Hofer (2003) modelled the distribution

of reptiles in Switzerland in response to climate and topography and found similar results for widely distributed species. Segurado and Araújo (2004), modelled the distributions of 44 species of amphibians and reptiles in Portugal, and found that more restricted and localised species were better modelled. In other words, there is a clear tendency towards a better model performance with restricted-range species groups, and widespread species are more difficult to model. Fielding and Bell (1997) noted that the greatest difficulty that ecological processes create for habitat models is that negative locations (i.e. absences) seem similar to positive locations (i.e. presences). Given that species with more restricted ecological niches are more localised and less frequent, it is expected that they will be better modelled and thus their distributions more easily predicted than more widespread species (Brotons et al., 2004). Stockwell and Peterson (2002) offered as a possible biological explanation that widespread species often show local or regional differences in ecological characteristics. Modelling all these sub-populations together would effectively overestimate the species ecological breadth and reduce model performance.

These six snakes species that could not be modelled may be termed “eurytopic” species at the scale of the current research, in the sense that are widely distributed and consequently able to adapt to a wide range of environmental conditions. Therefore, these species may not be limited by any of the measured predictive factors at the scale at which the model was fitted (Brotons et al., 2004).

The adaptability and hence the distribution of snake species may relate to differences in the way the snakes handle their ectothermal condition. A snake has the option of being entirely passive by allowing its body temperature (T_b) to be the same as the environment (thermoconformers), or it can take actions to maintain a relatively

constant T_b by behavioural means (thermoregulators). There is a continuum between the two extremes. In this respect, thermoregulators can be active over a longer time interval, be more effective competitors and be better able to elude predators (Pianka, 1996). Consequently, thermoregulators should be more adaptable to different environments and could be expected to present larger distributional ranges. Such a pattern in the relationship between the distribution of the Spanish snakes and their thermal biology was not found in the current study. Table 4.7 summarizes the different strategies of body temperature control in the Spanish snakes. In this respect, (Heatwole, 1976: 36) defined thigmotherms as “the ectotherms which depend primarily upon heat exchange with the substrate for maintenance of body temperature” while heliotherms are “those ectotherms which depend primarily upon radiant energy for their body heat”. Note that, as discussed above, thermoconformity and thermoregulation represent the ends of a spectrum of thermal biology where a species usually is neither a complete conformer nor a complete regulator (Pough et al., 2001).

Table 4.7: Thermal biology for the thirteen Spanish snakes.

Sources: Blázquez and Pleguezuelos (2002); Gosá (2002); Pleguezuelos and Honrubia (2002); Pleguezuelos (2003); Brito (2004); Feriche (2004); Galán (2004); Santos (2004); Santos and Pleguezuelos (2004); Pleguezuelos (2005).

	Species	Thermal biology
Not Modelized Species	<i>Coronella girondica</i>	Thermoregulator (thigmotherm)
	<i>Natrix maura</i>	Thermoconformer
	<i>Natrix natrix</i>	Thermoconformer
	<i>Vipera latastei</i>	No Data
	<i>Elaphe scalaris</i>	No Data
	<i>Malpolon monspessulanus</i>	Thermoregulator (heliotherm)
	Modelized Species	<i>Coronella austriaca</i>
<i>Macroprotodon brevis</i>		Thermoregulator (thigmotherm)
<i>Hemorrhois hippocrepis</i>		No Data
<i>Elaphe longissima</i>		No Data
<i>Vipera aspis</i>		No Data
<i>Coluber viridiflavus</i>		No Data
<i>Vipera seoanei</i>		Thermoregulator (heliothermic)

4.2.1.1. Not-Modelled widely distributed snakes

The wide distributions of *Natrix natrix* and *Natrix maura* are probably more determined by their association to water bodies than to climate, at least at the scale of this study (Figure 4.4). These species spend most of their life linked to open water in rivers, lakes and marshes (Santos, 2004). A strong signal may not result when their distribution is associated to climate because the climate signal is strongly moderated by their aquatic habits that allow them to behave as thermoconformers with water, showing variations of body temperature similar to that of the water in which they live. *Coronella girondica* also showed wide distribution over the whole Iberian Peninsula. The climatic signal for this species was particularly weak (Table 4.6). A possible explanation is a strong response to key resources, because other reptiles are the exclusive prey for this species (Santos and Pleguezuelos, 2004).

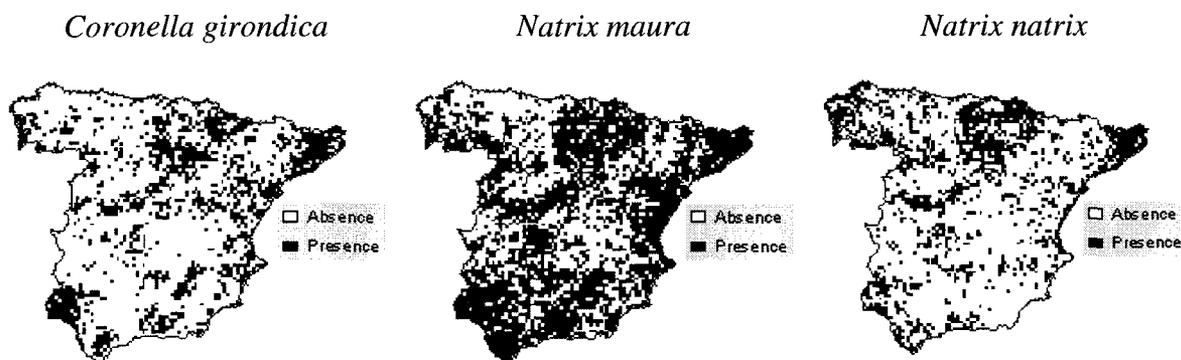


Figure 4.4: Distributions of the Spanish snakes that showed weak relationships with the variables used in the current research and were widely distributed

The local availability of these key resources (reptiles, aquatic habitats) not climatic factors, appear to be of overriding importance in determining the distribution ranges for these three species (Guisan et al., 2002).

4.2.1.2 Not-Modelled widely distributed snakes within the Mediterranean region

As shown in Figure 4.5, *Vipera latastei*, *Elaphe scalaris* and *Malpolon monspessulanus* are all widely distributed over the Spanish Iberian Peninsula, but they are more strongly present in the Mediterranean region than in the northwest. The Mediterranean region is characterized by abundant high radiation, mild winters on the coast, severe winters inland, and extremely irregular rainfall. The Spanish North Western region, where, they have very limited ranges, is part of the Spanish Eurosiberian region, and has a similar climate to most of western Europe, with mild winters, cool summers, moist air, and frequent precipitation during the year. It is evident that a climatic signal is emerging from their current distribution and the logistic analysis showed higher R^2 for these species (Table 4.6) than for the three already discussed. Nonetheless, the signal was not strong enough to produce an adequate model.

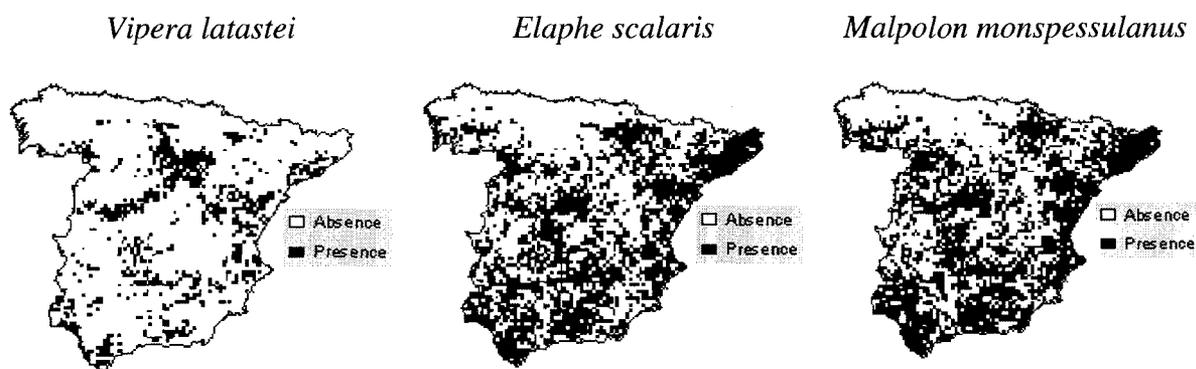


Figure 4.5: Distributions of the Spanish snakes that showed weak relationships with the variables used in the current research and were widely distributed within the Mediterranean region

The effects of climate change for these six widely distributed species probably will not be serious. Because all these species are able to exploit a substantial range of environments, they have margins to react to the changes in habitat that global warming is

likely to produce within Spain. While they might be extirpated from part of their current range, a large amount of climate change would be necessary to seriously threaten their presence in Spain.

4.2.2 Snakes amenable to be modelled

During the model building process, ten replications were used for each species from which the best sample was selected to project the snake's distributions. Table 4.8 provides a summary of the variables that entered into these best models and the order that they followed. Precipitation entered as the primary factor in five models, and temperature in two. The relation for these factors was positive for all the seven models. In all samples, except for *Coluber viridiflavus*, the first variable entering into the model was the same in 8 to 10 replications. For *Coluber viridiflavus*, summer precipitation entered as the primary factor in six replications while spring precipitation entered firstly in the remaining ones. Note that both summer and spring precipitation are highly correlated with each other.

Because forward stepwise selection was applied, it was not possible to give an ecological explanation of why variables other than the first ones entered into the models. In stepwise selection, the entrance of secondary variables is evaluated once the variance for variables already selected has been controlled (Hoshmer and Lemeshow, 2000). James and McCulloch (2002) pointed out this limitation when interpreting, from a biological perspective, results based on stepwise selection. The output from regression analysis do not tell that the variables in the final model are in fact important to the species, just that the variables are jointly related to the presence/absence of the species.

Biological cause cannot be reliably inferred from the variables selected. For example, as shown in Table 4.8, elevation was selected as a fourth variable entering into the *Vipera aspis*' models. Once the variance from summer precipitation, maximum autumn temperature and annual precipitation has been controlled, there is a residual variation leftover for which elevation provides the most significant statistical correlation. Because it is explaining a residual, a biological interpretation of the direct effect that elevation might have over the distribution of *Vipera aspis* cannot be assumed to act in the same direction.

Table 4.8: Variables and order followed when entered into the logistic models

Species	First	Second	Third	Fourth
<i>Coronella austriaca</i>	Spring precipitation	Maximum spring temperature	X	X
<i>Elaphe longissima</i>	Summer precipitation	Minimum summer temperature	X	X
<i>Vipera seoanei</i>	Winter precipitation	Maximum summer temperature	X	X
<i>Coluber viridiflavus</i>	Summer precipitation	X	X	X
<i>Vipera aspis</i>	Summer precipitation	Maximum autumn temperature	Annual precipitation	Elevation
<i>Macroprotodon brevis</i>	Maximum winter temperature	Elevation	X	X
<i>Hemorrhois hippocrepis</i>	Maximum winter temperature	Summer precipitation	X	X

As shown in Figure 4.6, climatic variables explained the distributions of all the snakes modelled more efficiently than topography. A probable explanation is that topography generally has an indirect effect on animal distributions by influencing local microclimates, with some of its parameters, like temperature, having a direct effect on reptiles' survival (Austin, 2002). Furthermore, topography might be a factor through an indirect effect on other features such as the type of soil or access to refuge. The model suggests that these features have low level importance relative to climate for the reptile

species considered. Alternatively, the integrity of such additional environmental features and their possible combinations might be lost when aggregating topographical data to the 10 x 10 km resolution (Guisan and Hofer, 2003).

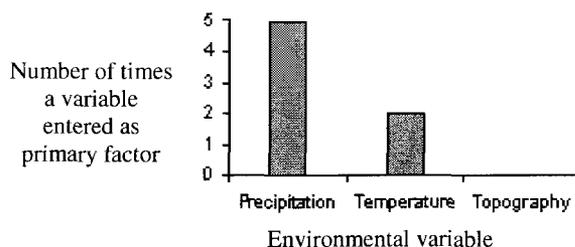


Figure 4.6: Importance of variables as primary factors determining snake distributions

Temperature is almost certainly the most important single physical factor in the ecology of reptiles because of their ectothermal condition (Heatwole, 1976). Ectotherms cannot maintain their body temperatures independent of environmental conditions. The functioning of snakes is limited in space and in time by the ambient temperature. Everything the animal does is affected by changes in body temperature, including activities that are critical to its survival, such as sprinting to escape a predator or striking a prey (Pough et al., 2001). Thus, night times and cold seasons present especially difficult conditions for ectotherms. Consequently, temperature might be considered as the most important direct factor delineating ectothermal animal distributions. Precipitation is likely to play a more indirect role. For example, Mayhew (1966, see Pough et al. 2001) found that breeding patterns in *Uma scoparia* (lizard) were correlated with rainfall, because it would induce sand-dwelling plants to germinate and produce the food utilized by insects which, in turn, were fed upon by the lizards.

The analyses indicate that the way climate and snakes' distributions are linked may differ depending on the biogeographic region occupied by the species. For Eurosiberian species, the primary predictor was precipitation. In contrast, temperature was the best predictor for Mediterranean species. This fact would suggest that distributional patterns for the snakes modelled are driven primarily by direct climate effects operating on physiological requirements for Mediterranean species, while for Eurosiberian species, climate may operate indirectly via food availability (Rodríguez et al., 2005).

4.2.2.1 Eurosiberian snakes: Precipitation as primary factor influencing distribution

For five species, precipitation and not temperature was the primary factor. As we have seen, temperature is important in all ectotherms but for these species it would appear that their distribution, at the scale of the current study, relates more to other factors, such as food availability. All snakes are predators (Pleguezuelos et al., 2002). Consequently, if precipitation effects on their distribution are related to food availability, these effects will be indirect and mediated by consumer biomass. In other words, if this hypothesis is correct, the indirect effects of climate on these snakes' distributions would occur through a process with at least three steps: climate determines production at the first trophic level (plants), which in turn determines production at the second trophic level (potential prey), which in turn influences the snakes' distributions (Rodríguez et al. 2005). An alternative explanation for the observed relationship between Eurosiberian species and precipitation is that the distribution of these species could be associated with plant cover, which in turn is determined by the amount of precipitation.

4.2.2.2 Mediterranean snakes: Temperature as primary factor influencing distribution

The distribution of two snakes was found to be influenced by temperature as primary factor. These two species are restricted to the Mediterranean biogeographic region and their Northern boundaries occur within the Iberian Peninsula. Both species, *Hemorrhois hippocrepis* and *Macroprotodon brevis* (Feriche, 2004; Pleguezuelos, 2005), are thermophiles. Consequently, these species would be restrained in their distribution.

4.3 Species projections and derived statistics

The results presented in this section (Figures 4.7 – 4.13) represent estimates of the potential changes in the distribution of areas suitable for the various snake species in 2020, as a result of climate change, and projections of possible changes in the distributions of snake species in 2020. It is doubtful that the maps will be accurate in their details; rather, they represent the general trends that the snakes' distributions will follow if the circumstances supposed by the Hadley climate projections are fulfilled. The results presented here are predictions derived from models (that is, from hypothesis). Model outputs represent what would occur if the premises of the climate change models were strictly correct, and the biological response characteristics were known precisely.

This section provides information on the current and potential distribution of the seven snakes modelled. The structure and the summary indices used were adapted from the “*Atlas of climate change effects in 150 bird species of the Eastern United States*” made by the U.S. Department of Agriculture (Matthews et al., 2004).

The distribution for each species is displayed in four maps. Map A indicates the current distribution based on Pleguezuelos et al. (2002). Map B shows the modelled

current distribution as reconstructed by the logistic regression analysis when the recent environmental dataset was implemented into the model. Map C shows the distribution of the suitability of habitat under the 2020 Hadley climate change scenario. Spatial distribution in 2020 was reconstructed in the same way as the modelled current distribution but implementing the future environmental dataset. Map D shows the distribution of change projected from the current distribution. Range lost (or “lost” in the map legend) was defined by Matthews et al. (2004: 8) as “the percentage of the current range of the species that no longer will be occupied under climate change despite potential gains elsewhere”. Matthews et al. (2004: 8) considered the range gained (or “gained” in the map legend) as “the potential gain in area as a percentage of its current range despite potential losses elsewhere”. In both cases, a cutpoint of 0.80 was established as the threshold to include an area as suitable habitat for a species in 2020.

Total range change is the combination of range gained and range lost and might be useful in the interpretation of potential shifts in range. A low value might mean that the snake is not affected at all by climate change or that the species migrates readily from one area to another. The separate estimations for range lost and range gained allows differentiation between these cases.

The restricted dispersal abilities of snakes were discussed in section 2.1.4. Based on this premise, the “suitable” category was defined as those areas where the conditions predicted by the model were suitable for the species but too far from their current locations to be reached in 2020 according to best estimates of maximum probable migration rates. In this respect, no field or theoretical studies have been done for the snakes of Spain. The migration distances were estimated based on an extrapolation

derived from the opinion of an expert in Spanish snakes (Table 2.2). Consequently, this is only an attempt to assess the limitation of the species in being able to migrate into all the areas predicted to be suitable by the models. Long-term field experiments might be carried out to address accurately the migration abilities of each species.

In the model summary are presented the Accuracy Index ($AI(\%)$), Coefficient of determination (R^2), *Specificity*, *Sensitivity* and Area under the *ROC* curve (*AUC*) of the best model selected from among ten replications (see section 3.3 for further details).

The model equation indicates the coefficients and the variables that entered into the logistic models. The order in which the variables are listed is the order in which they entered into the model, that is, the variable that appears after the constant was the first to enter into the model and therefore the most important. The model equation presented is a simplification of the real logistic model, which is represented by the equation:

$$f(z) = \frac{1}{1 + e^{-z}}$$

Only the logit (value of “z”) is presented in these Figures.

Finally, note that in this section, the term “accurate” when describing the reliability of the models has been used following the definition by Zar (1984, see Morrison and Hall 2002: 51): “Accuracy is the nearness of a measurement to the actual value of the variable being measured”.

All photos were obtained from the “*Atlas y libro rojo de los anfibios y reptiles de España*” (Pleguezuelos et al. 2002). J.L. Barbadillo made available the majority of the species photographs; J. Bosch supplied the *Macroprotodon brevis* photo.

4.3.1 *Vipera seoanei*

The model underestimates the current occurrence of Seoane's viper in those populations closer to the Portuguese border (Figures 4.7 A and B), but the overall patterns predicted by logistic regression are reasonably accurate.

This endemic Iberian species appears to be limited by winter precipitation. Under the climate change scenario, the area with higher winter precipitation will broaden in the western portion of the species' distribution (Galicia) by 2020 while the area will remain the same or even decrease (Appendix 5) in its eastern distribution. Consequently, under this scenario Galicia might become more habitable while the eastern patches turn less habitable. Furthermore, a zone in the central western portion of Spain along the Portuguese border (north of Cáceres) is projected to become habitable (Figure 4.7 C).

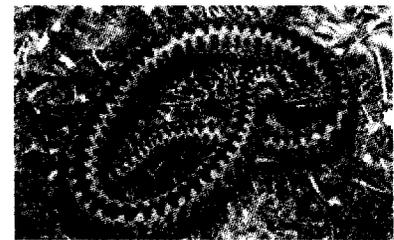
Figure 4.7 D takes into account the limited dispersal abilities of the species and projects the areas from which it will be extirpated, which amounts to 46.5 % of the area currently occupied, and the areas into which it could migrate which amounts to 55.8 % of its current range. The net range would be + 9.3 %. The Northern Cáceres area and some other areas of new suitable habitat are too remote from currently occupied areas to be colonized by this species.

4.3.2 *Vipera aspis*

The model captured a core patch of the species distribution in the north eastern portion of the study area, but it failed to predict its occurrence in substantial parts of its north western distribution (Figures 4.8 A and B). Nonetheless the patterns predicted by the model are moderately accurate.

***Vipera seoanei* (Lataste, 1879)**

Víbora de Seoane, Seoane's viper



Model Summary

AI (%)	95.6		
R ²	0.63	Sensitivity(%)	Specificity(%)
AUC	0.97	64.1	98.2

Model Equation $Z = [7.00 + 0.009 (\text{Winter precipitation}) - 0.47 (\text{Maximum summer temperature})]$

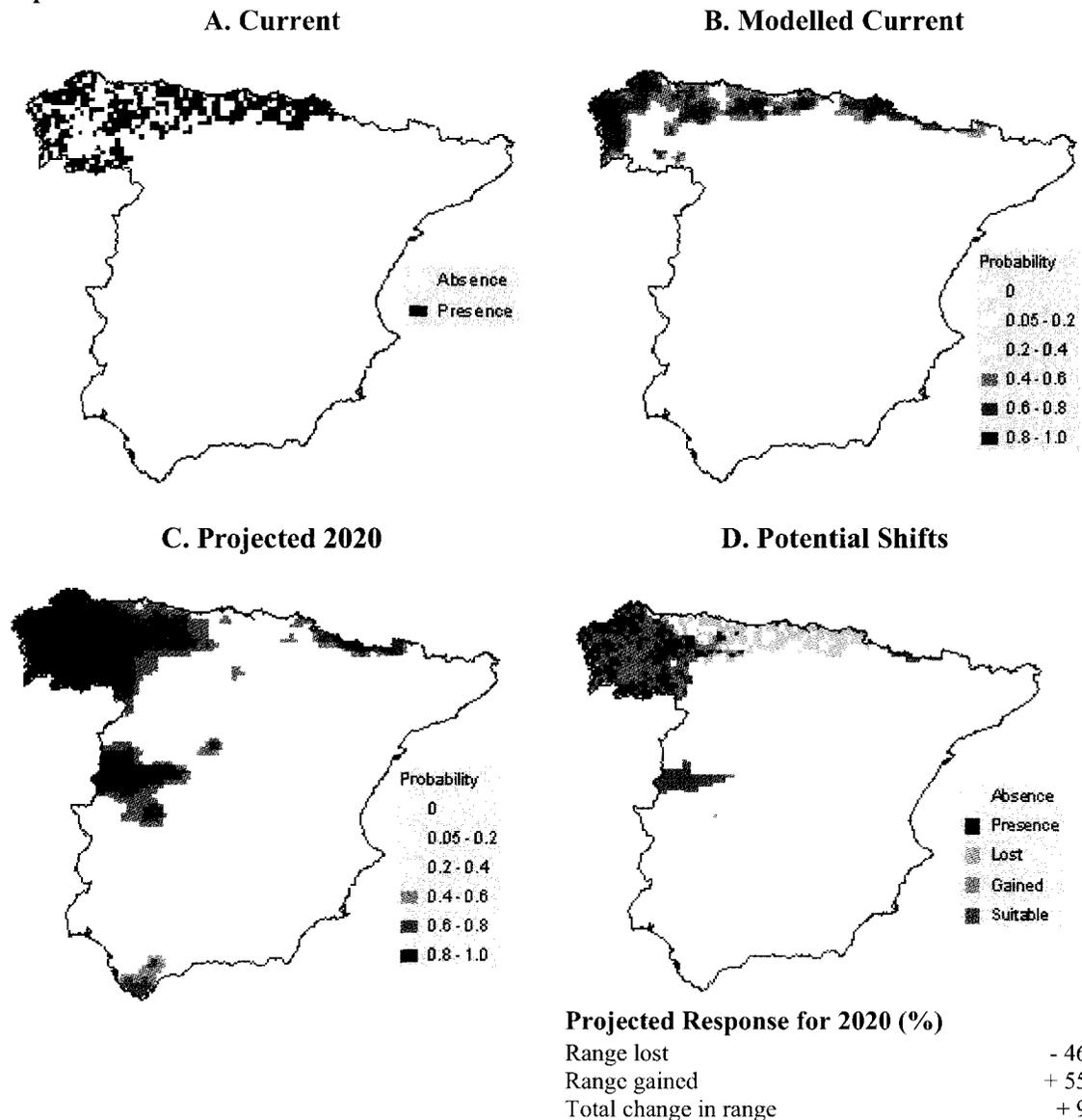
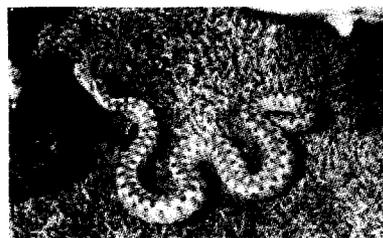


Figure 4.7: Current distribution and projections derived from the logistic regression for *Vipera seoanei*.

***Vipera aspis* (Linnaeus, 1758)**

Víbora aspid, Asp viper

**Model Summary**

AI (%)	96.2		
R ²	0.53	Sensitivity(%)	Specificity(%)
AUC	0.96	58	98.7

Model Equation $Z = [40.16 + 0.037 (\text{Summer precipitation}) - 2.05 (\text{Maximum autumn temperature}) - 0.007 (\text{Annual precipitation}) - 0.007 (\text{Elevation})]$

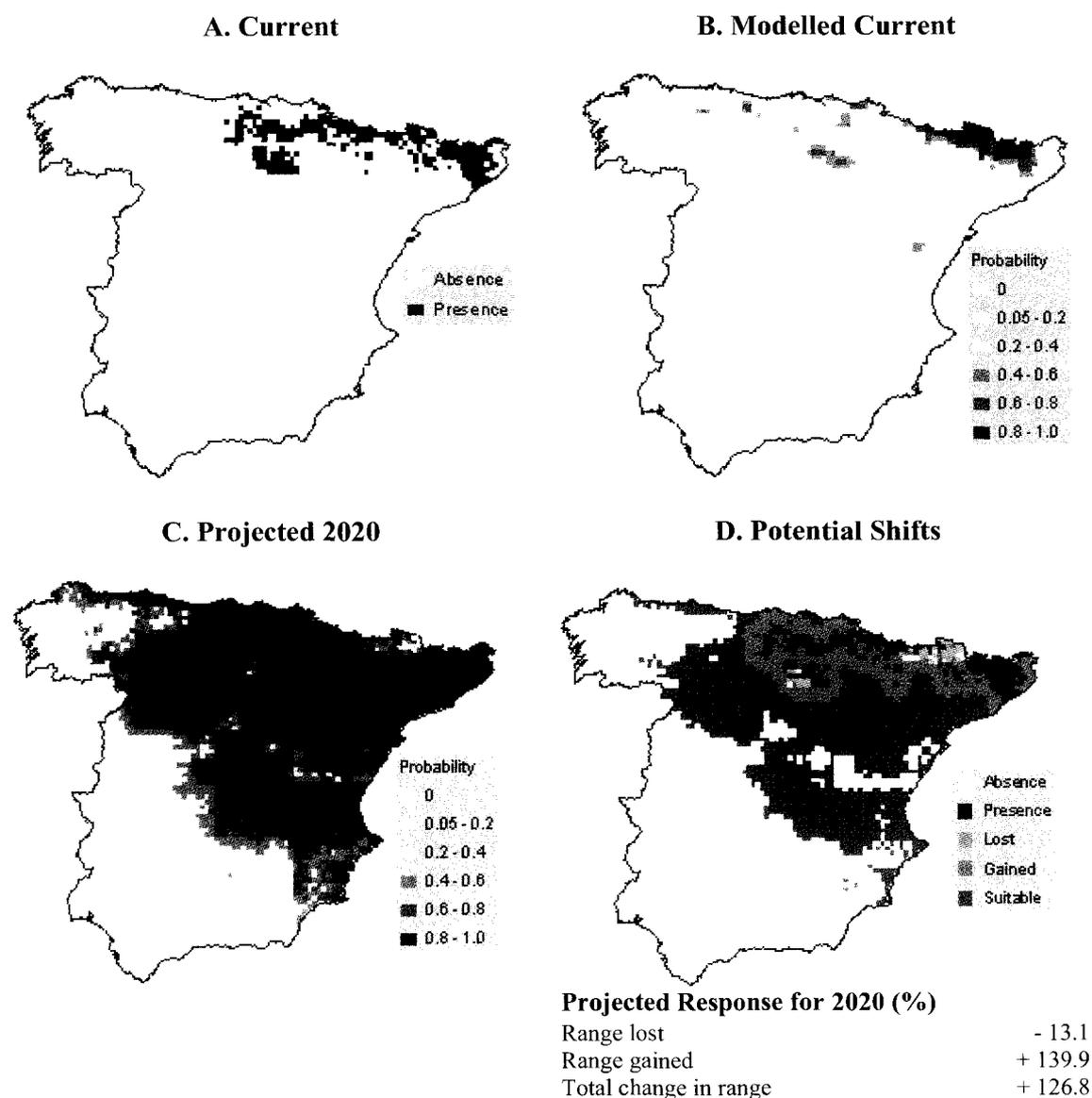


Figure 4.8: Current distribution and projections derived from the logistic regression for *Vipera aspis*

The model predicted large increases in suitable habitat (Figure 4.8 C) apparently because of the enlarging distribution of areas with higher summer precipitation in 2020 (Appendix 3). This projection seems certainly overestimated. When the limited dispersal abilities of the species are taken into account the increase in area occupied by 2020 is in the range of 140 % (Figure 4.8 D).

4.3.3 *Macroprotodon brevis*

The model failed to predict the core population of this species in the Iberian southwest (Figures 4.9 A, B). This problem might be produced in part because the burrowing habits of this snake make it difficult to detect, limit the number of sightings (Pleguezuelos, 2005), and lead to some degree of bias during the sampling process. The hooded snake seems to be restricted by maximum winter temperature. As shown in Figure 4.9 C, the western portion of the species' distribution range might become less habitable. The area where maximum winter temperatures are modelled to be suitable for the species in 2020 are predicted to expand in south eastern Spain (Appendix 5). As a result, there might be little change in total range because new colonized areas in the east balance western extirpated populations (Figure 4.9 D). New northern suitable habitats that may emerge are too distant from current populations to be reached by this species, and potential migration corridors will not exist by 2020.

***Macroprotodon brevis* (Günter, 1862)**

Culebra de cogulla, Hooded snake.



Model Summary

AI (%)	90.9		
R ²	0.29	Sensitivity (%)	Specificity (%)
AUC	0.88	8.9	99.5

Model Equation $Z = [-15.21 + 0.88 (\text{Maximum winter temperature}) + 0.003 (\text{Elevation})]$

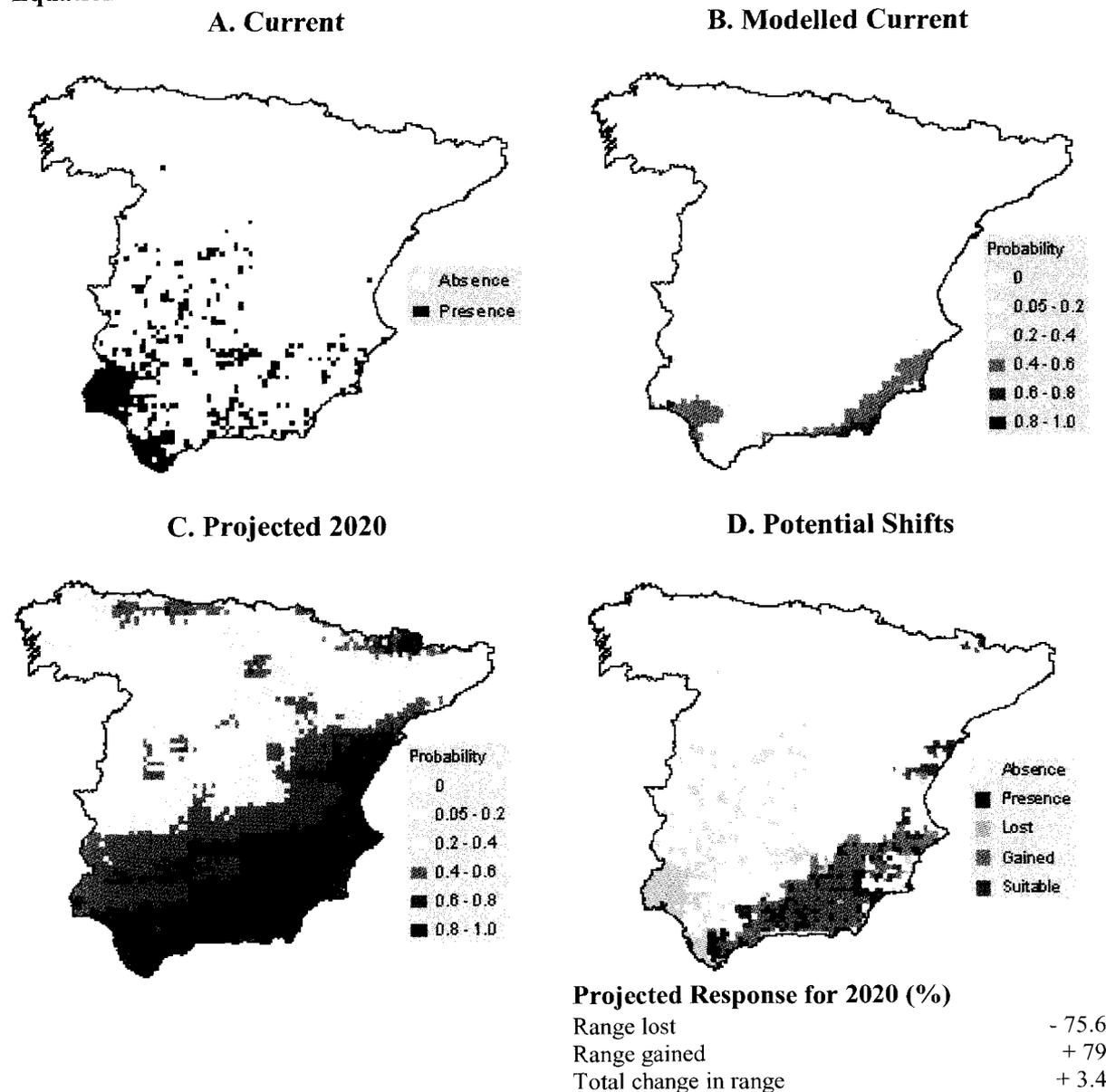


Figure 4.9: Current distribution and projections derived from the logistic regression for *Macroprotodon brevis*

4.3.4 *Elaphe longissima*

Although most of the northern distribution of this Eurosiberian species is well modelled, the model failed to capture its extreme northeastern patch of presence (Figures 4.10 A, B).

This species seems to be most limited by summer precipitation. Summer precipitation will remain more or less constant throughout the current species' distribution area (Appendix 3) as modelled by the logistic regression. Consequently, under this climate change scenario almost the same areas as were predicted as habitable will remain habitable (0.8-1.0 probability) for the species in 2020 (Figure 4.10 C).

Under the Hadley climate change assumption this species might suffer 90 % reduction in distributional area (Figure 4.10 D). Given the inaccuracy in the prediction of the current distribution (Figure 4.10 B), it seems probable that the 90 % reduction in area inhabited is substantially overestimated. Nonetheless, the species is expected to remain restricted to a small area in the Pyrénées along the border with France.

4.3.5 *Hemorrhois hippocrepis*

The model captured the core of the species distribution in the southwestern portion of the study area and most coastal populations, but it failed to predict its occurrence in the interior areas (Figures 4.11 A and B). The patterns predicted by the model can be considered as moderately accurate.

Under the climate change scenario, the coastal regions where the species is currently present remain habitable while the interior and northern Peninsula will become less habitable (Figure 4.11 C).

***Elaphe longissima* (Laurenti, 1768)**
 Culebra de Esculapio, Aesculapian snake.



Model Summary

AI (%)	98.2		
R ²	0.46	Sensitivity (%)	Specificity (%)
AUC	0.96	25	100

Model Equation $Z = [-15.14 + 0.03 (\text{Summer precipitation}) + 0.48 (\text{Minimum summer temperature})]$

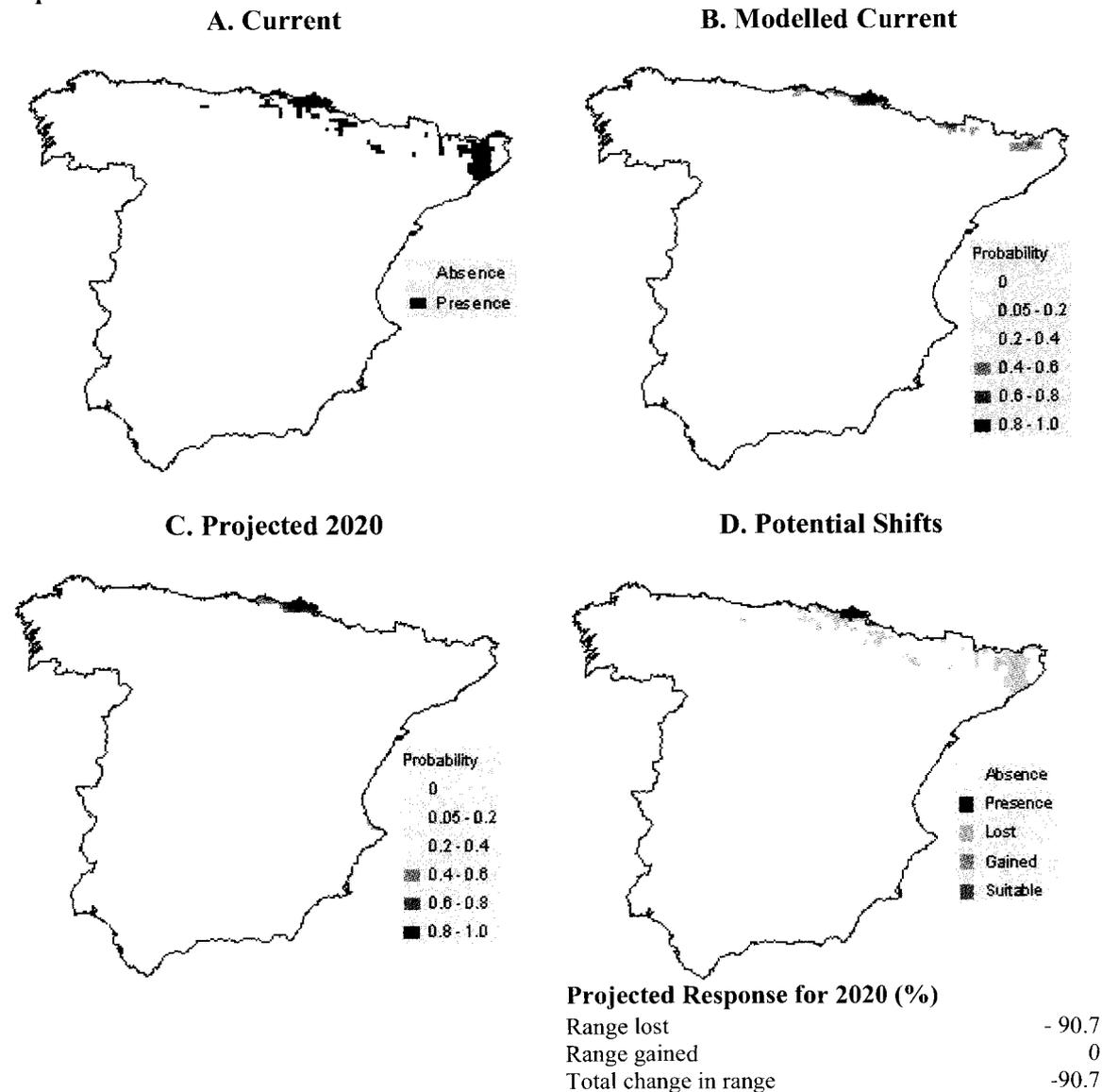
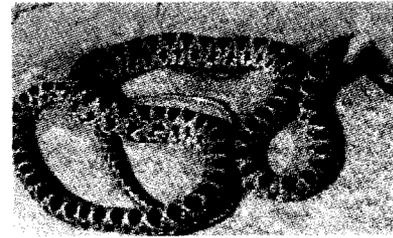


Figure 4.10: Current distribution and projections derived from the logistic regression for *Elaphe longissima*

***Hemorrhoids hippocrepis* (Linnaeus, 1758)**

Culebra de herradura, Horseshoe snake.



Model Summary

AI (%)	83.8		
R ²	0.43	Sensitivity(%)	Specificity(%)
AUC	0.86	34	96.4

Model Equation $Z = [-6.9 + 0.54 (\text{Maximum winter temperature}) - 0.012 (\text{Summer precipitation})]$

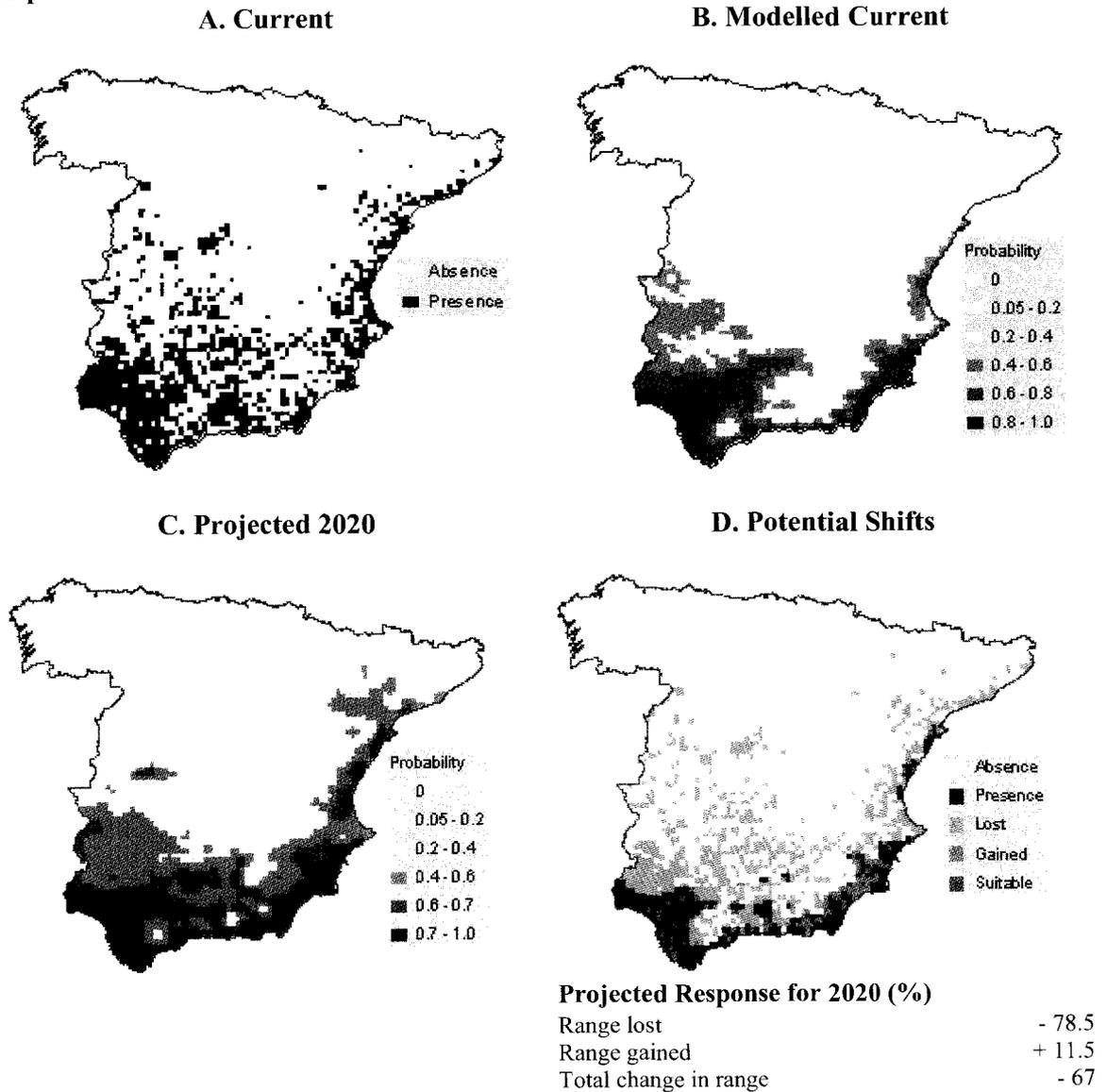


Figure 4.11: Current distribution and projections derived from the logistic regression for *Hemorrhoids hippocrepis*

The model projects a marked contraction from the northern portion of the range of this temperature-sensitive species. 78.5% of the area that it currently occupies is predicted to be lost (Figure 4.11 D). Indeed, this trend of contraction in the northern populations of this species has been noticed in recent years by Pleguezuelos and Feriche, (2002) who pointed to global change as a possible explanation.

4.3.6 Coronella austriaca

The model slightly underestimated the current occurrence of the Smooth snake in the southern portion of its range (Figures 4.12 A, B). However, patterns predicted by the model are relatively accurate.

The projections for this species, using the model that predicts complete extirpation (Figure 4.12 D) are almost certainly overestimates. A possible explanation could be the species selection of microhabitats that may reduce the sensitivity of the models to find relationships between distribution and climate.

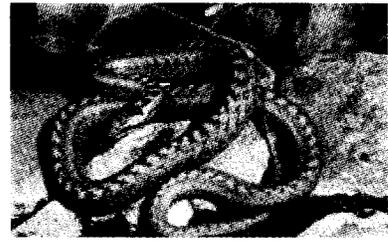
Because spring precipitation is not projected to change in 2020, the drastic reduction predicted for this species might be associated, besides other factors not considered (e.g. food availability, forest cover), with an expanding distribution of warmer maximum spring temperatures (Appendix 2). Under the climate change scenario all the areas currently occupied are projected to become less habitable (Figure 4.12 C).

4.3.7 Coluber viridiflavus

The patterns predicted are relatively accurate (Figure 14.13 A, B), although, the model slightly underestimated the current occurrence of this species in the southern part of its distribution.

***Coronella austriaca* (Laurenti, 1768)**

Culebra lisa europea, Smooth snake.



Model Summary

AI (%)	90.5		
R ²	0.39	Sensitivity(%)	Specificity(%)
AUC	0.89	26.9	97.9

Model Equation $Z = [-0.81 + 0.01 (\text{Spring precipitation}) - 0.32 (\text{Maximum spring temperature})]$

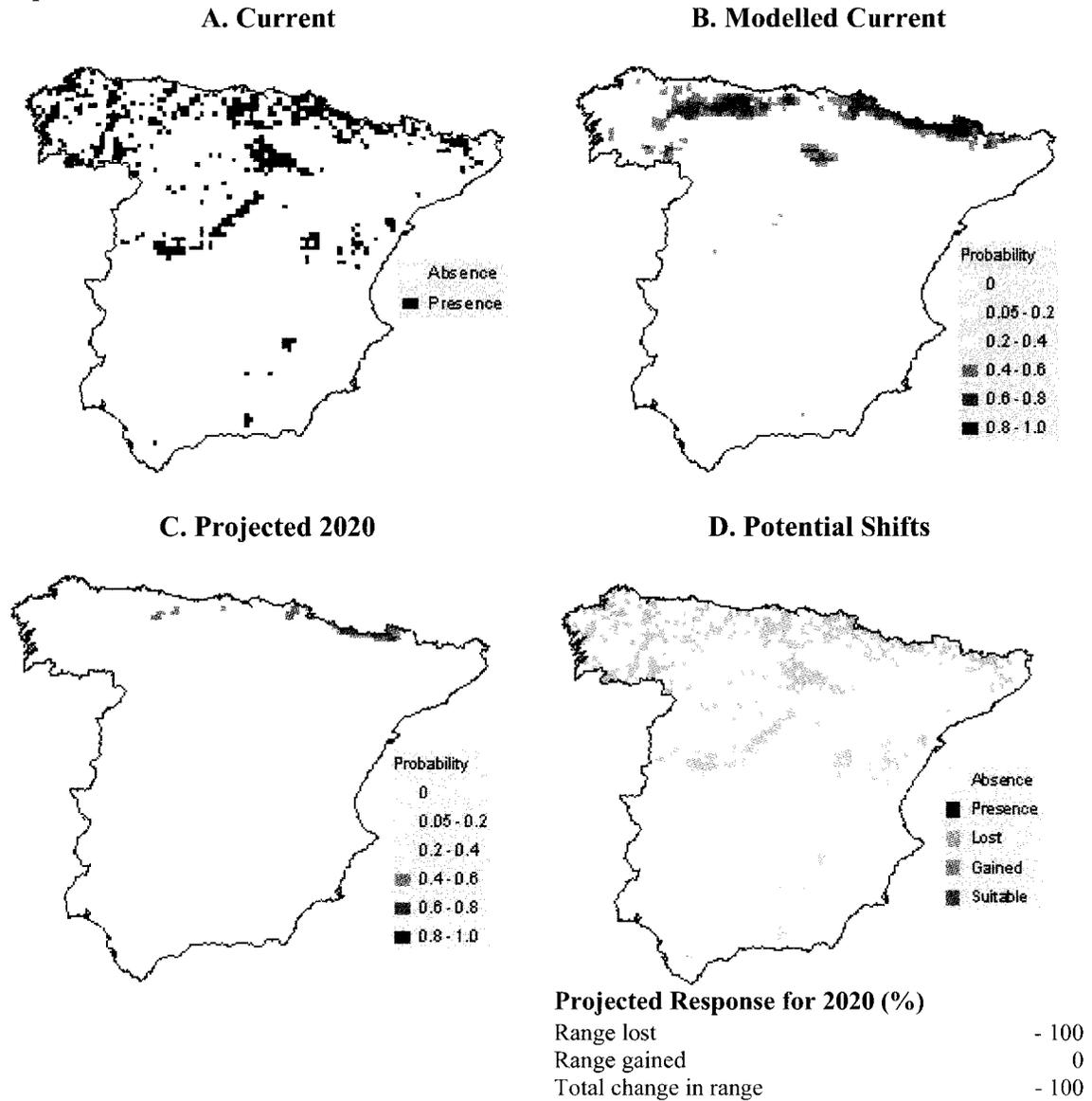


Figure 4.12: Current distribution and projections derived from the logistic regression for *Coronella austriaca*.

***Coluber viridiflavus* (Lacepède, 1789)**

Culebra verdiamarilla, European whip snake.

**Model Summary**

AI (%)	98.9		
R ²	0.58	Sensitivity(%)	Specificity(%)
AUC	0.98	44	100

Model Equation $Z = [-9.04 + 0.03 (\text{Summer precipitation})]$

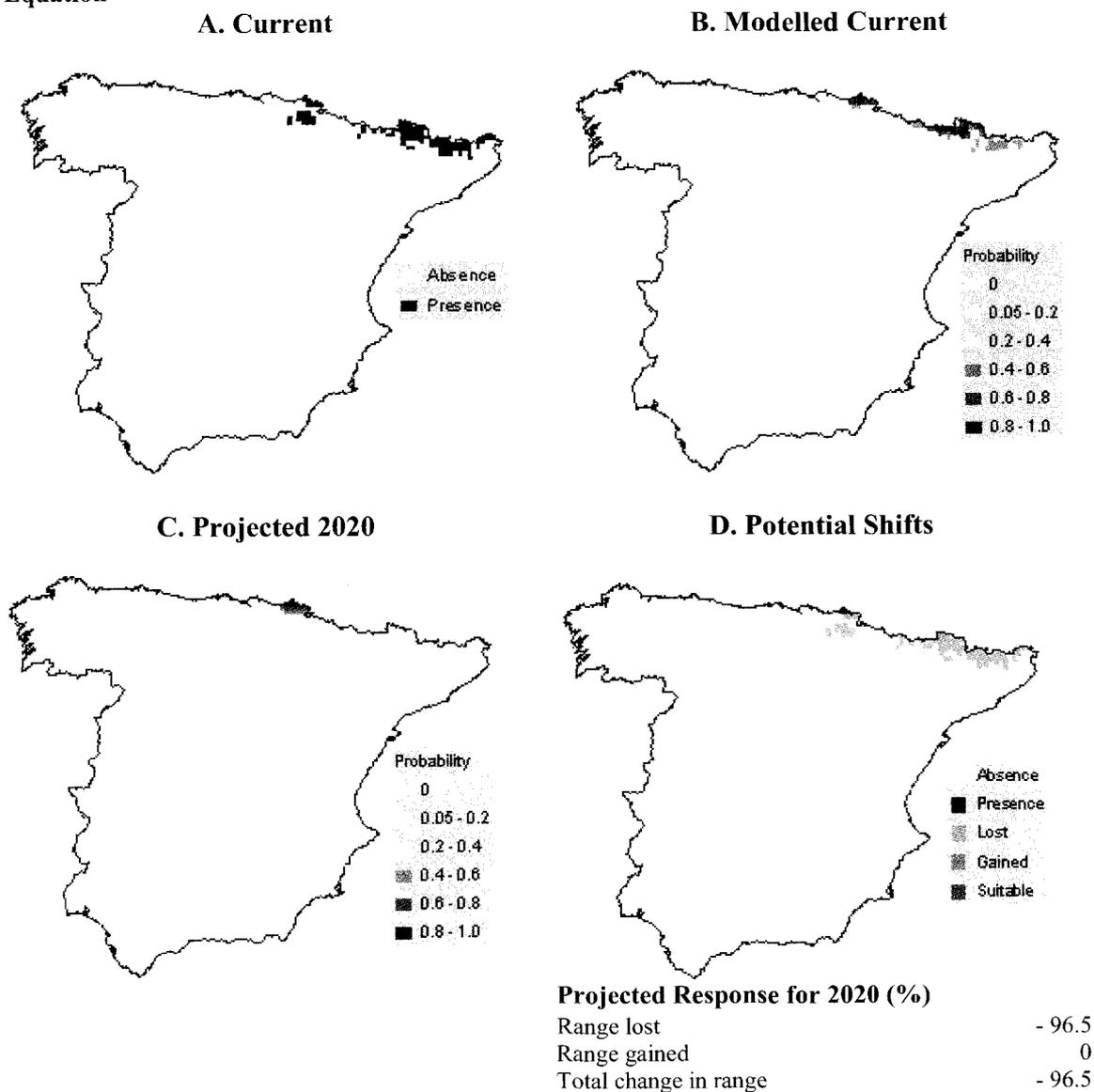


Figure 4.13: Current distribution and projections derived from the logistic regression for *Coluber viridiflavus*

This snake seems to be limited by summer precipitation. As shown in Figure 4.13 C, only the most north western area of its current distribution might remain habitable in 2020. As a result, the European Whip snake is predicted to be severely affected by climate change, losing 96.5% of its current distribution in Spain (Figure 4.13 D)

4.4 Evaluation of models

A general unexplored question in species modelling (Brotons et al., 2001) is: how dependent is the accuracy of a modelling approach on the ecological characteristics of the species and how do these interact with species prevalence to determine model performance. So far we have seen that as a consequence of particular ecological characteristics of some Spanish snakes it was not always possible to produce adequate models. In particular, it was not possible to develop models of the species that were widely distributed in Spain.

In this study, five statistical methods were generated to evaluate model performance. As described in section 3.3.4, *AUC* measure from an *ROC* curve is useful in evaluating the ability of the models to distinguish between presence and absence in a threshold-independent fashion. Furthermore, the *AI(%)* is an accuracy index which count the errors produced by the models against the total number of presence and absence to be detected. In the same manner, *specificity* (true positives) and *sensitivity* (true negatives) measure the proportion of sites at which the observations and predictions agree. Finally, the coefficient of determination gives a statistical measure of how well the presence/absence is explained by the predictors.

Models involving measures derived from a confusion matrix such as $AI(\%)$, *specificity* or *sensitivity* have been widely applied in environmental sciences. On the other hand, methods involving *ROC* curves have been infrequently applied to ecological data (Manel et al., 2001). The current research seems to provide a good opportunity to test these performance indicators, especially in terms of prevalence of the species.

Prevalence has been defined as the frequency of occurrence in a dataset of the target organism (Fielding and Bell, 1997). Indices to assess model performance should be independent of the frequency of occurrence. However, indications pointing out that predictive accuracy of habitat models might be affected by prevalence have been stressed by several studies (e.g. Araújo and Williams, 2000, Pearce and Ferrier, 2000, Manel et al., 2001; Stockwell and Peterson, 2002, Brotons et al., 2004). In Figure 4.14, prevalence was correlated (*Spearman's* rank correlation coefficient) with model performance measurements.

Although prevalence is measured on a 0 to 1 scale, in this sample, the highest prevalence value was 0.2, reached by *Hemorrhoids hippocrepis* (Table 4.9). Consequently, plots were scaled based on this maximum value.

Table 4.9: Values of prevalence and the five model performance measures applied for each modeled snake. Models are ranked from minimum to maximum prevalence values.

	Prevalence	R ²	AI	AUC	Specificity	Sensitivity
<i>Coluber viridiflavus</i>	0.02	0.58	0.98	0.98	1.00	0.44
<i>Elaphe longissima</i>	0.02	0.46	0.98	0.96	1.00	0.25
<i>Vipera aspis</i>	0.06	0.53	0.96	0.96	0.98	0.58
<i>Vipera seoanei</i>	0.08	0.63	0.95	0.97	0.98	0.64
<i>Macroprotodon brevis</i>	0.09	0.29	0.90	0.88	0.99	0.08
<i>Coronella austriaca</i>	0.10	0.39	0.90	0.89	0.98	0.26
<i>Hemorrhoids hippocrepis</i>	0.20	0.43	0.83	0.86	0.96	0.34

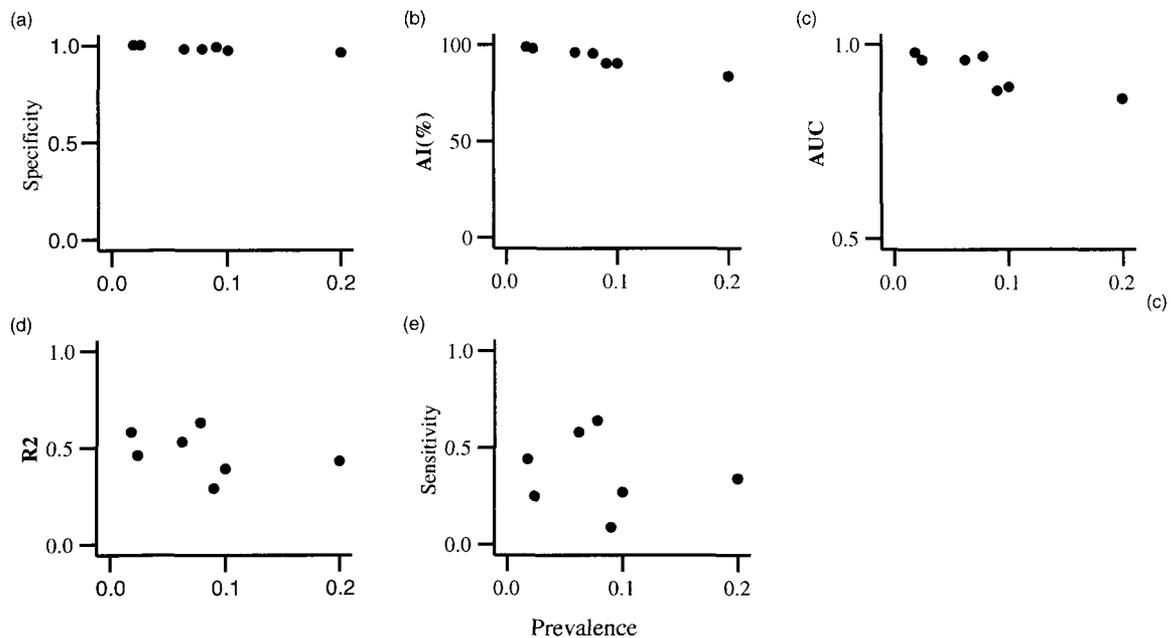


Figure 4.14: Spearman correlations between prevalence and the different model performance indices used. (a) *Specificity*, (b) *AI (%)*, (c) *AUC*, (d) R^2 and (e) *Sensitivity* of the seven Spanish snake models in relation to their occurrence in the calibration dataset.

As shown in Figures 4.14, *specificity* ($r_s = -0.87$, $P = 0.01$), *AI(%)* ($r_s = -0.85$, $P = 0.016$) and *AUC* ($r_s = -0.84$, $P = 0.016$) were negatively correlated to the frequency of species occurrences. This means in the case of *specificity* (and probably *AI(%)*) that absences were more effectively predicted as the prevalence increased. Furthermore, snakes with fewer occurrences, such as *Coluber viridiflavus* or *Elaphe longissima*, produced unjustified high values of *specificity* and *AI (%)* (Table 4.9). On the other hand, R^2 ($r_s = -0.61$, $P = 0.148$) and *sensitivity* ($r_s = -0.21$, $P = 0.645$) were not affected by prevalence.

In this respect, there is still disagreement on the role of prevalence in model performance. For example, Araújo and Williams (2000) found that prevalence negatively affected *specificity* and positively affected *sensitivity*, while Manel et al. (2001) found that *AUC* was independent of prevalence, but they recognized that erroneous predictions

could be generated when the distribution of scarce organisms were predicted. Finally, Brotons et al. (2004) found that higher prevalence values were associated with higher *AUC* values.

A critical assessment of the effects of prevalence on model predictive accuracy is problematic because prevalence is likely to vary both with species ecological characteristics and sampling effort. Less tolerant species will tend to be less frequent and therefore fewer records will be available than for widely distributed species. On the other hand, lower sampling effort may also decrease prevalence and will affect model performance (Brotons et al., 2004).

Whatever the reason and the sign of the relation between prevalence and model performance, a visual assessment of the potential current distribution modeled for the Spanish snakes does not seem as highly accurate as *AI(%)*, *specificity* and *AUC* suggest. The apparent overestimation produced by *AI (%)* and *specificity* is associated with its high dependence on the presence/absence rate. This rate was always unbalanced towards a high number of absences. Nevertheless *AI(%)* and *specificity* were not able to detect this disequilibrium. In other words, if a sample mostly formed of absences is considered, these indices associate the same value to a model detecting presences as to a model detecting absences.

In the same manner as *specificity* was affected by few presences, *sensitivity* might be affected if the frequency of occurrences were significantly higher than the absences. From this point of view, the coefficient of determination seems to be the most appropriate index to measure model performance, although the R^2 in logistic regression entails other statistical problems discussed in section 2.3.3.1.

In conclusion, the perfect index to assess model performance does not seem to exist. The kind of data and the modelling technique applied should determine partially the statistical method chosen to evaluate model performance. In addition, more than one index of performance should be utilized, if that is possible.

4.5 Prioritization of sites

The current research has presented the potential sites in 2020 where Spanish snakes could exist from a physiographic perspective, all other factors being ignored, even if they might be important. Six snakes were so widely distributed that there were not adequate differences in the values of variables between presence and absence sites for them to be modelled. Nonetheless, concern about them should be minor when compared with more restricted species because they are likely to have greater ability to face likely changes in their habitats, at least at the Spanish scale.

Many ecological studies on species habitat preferences usually do not deal with the management implications of their findings (Newbold and Eadie, 2004). In this respect, I tried to address the question of how much more effective could a conservation planner be with the additional information given by my results. Thus, two prioritization maps were generated to rank areas from a physiographic perspective, according to their importance in sustaining Spanish snakes. These maps might allow conservation planners to manage the species.

In Figure 4.15 (a) the suitable areas where the snakes might be able to migrate and areas that will remain suitable under the Hadley climate change scenario are presented. The western border with France, between Guipuzcoa and Navarra, seems adequate for

Coluber viridflavus, *Vipera aspis* and *Elaphe longissima*. Furthermore, the Levante region (central and southern Mediterranean coast) harbours several spots that might be important for *Macroprotodon brevis* and *Hemorrhois hippocrepis*.

Figure 4.15 (b) shows areas that might be suitable but are too distant from current distribution locations to be reached by the species by 2020 because of their dispersal restrictions. Consequently, artificial tools (i.e. human transportation) might be applied if it were judged to be desirable to locate the snakes into these patches. The large region gained by *Vipera aspis* in the Spanish North-central sector dominates this map. Two areas close to the Northeastern Portuguese border (León and Zamora) might be important from a physiographic perspective for *Vipera aspis* and *Vipera seaonei*. The central eastern Iberian Peninsula also might harbour two patches close to the Mediterranean shores (Valencia) where *Vipera aspis* and *Macroprotodon brevis* could find suitable conditions for their introduction.

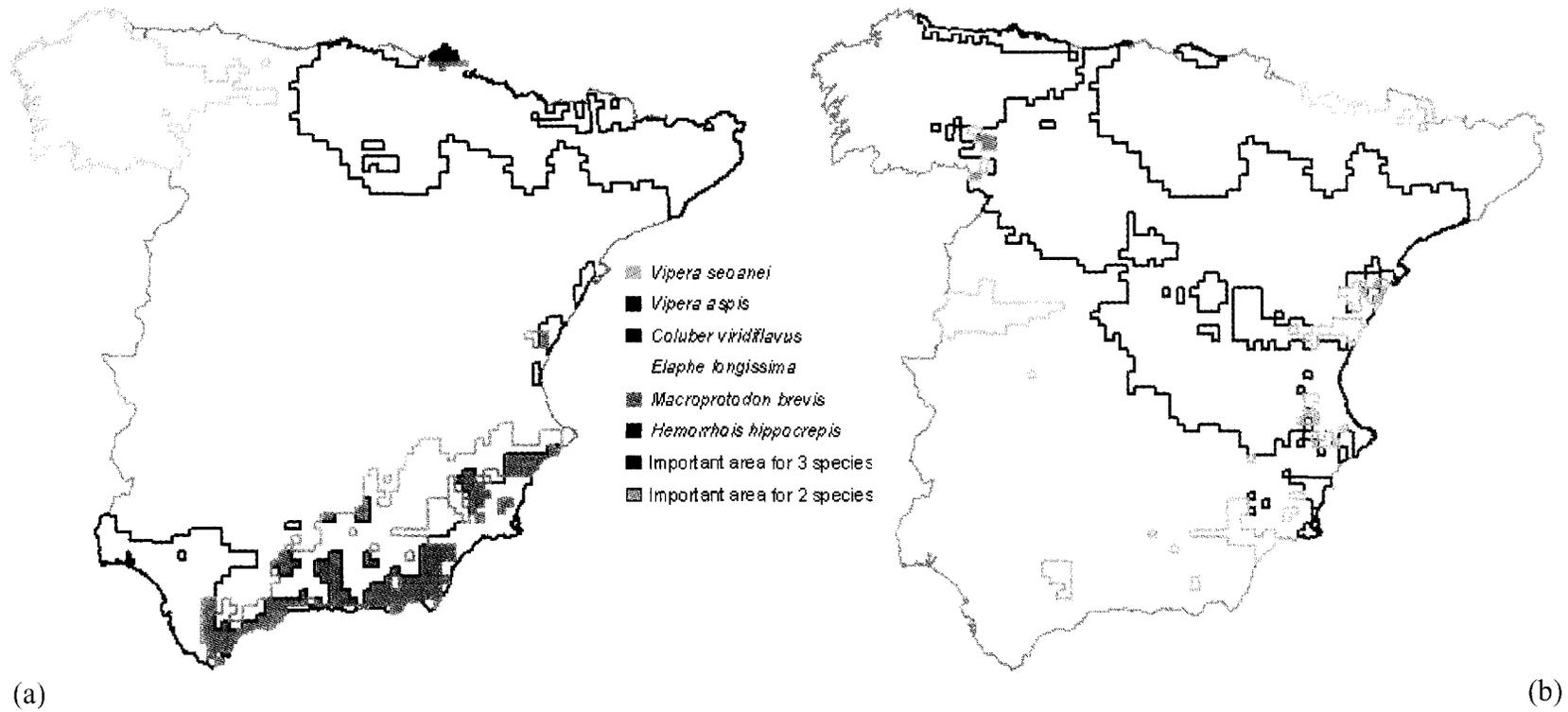


Figure 4.15: Prioritization sites of Spanish snakes under a future climate change scenario from a physiographic perspective.
(a) Areas that species might reach through migration.
(b) Suitable areas but too far from their current distribution to be reached in 2020.

CHAPTER 5

THESIS SUMMARY AND CONCLUSIONS

Modelling is as yet the only available tool for predicting the direction and magnitude of the effects of climate change (Teixeira and Arntzen, 2004). It is not possible to validate on the ground the outcomes produced. Consequently, judgments must be made based on statistical techniques.

Many tools are available to model species distributions. Logistic regression is probably the most commonly applied when using presence/absence data but this does not necessarily mean that it is the best. This statistical method comes, like all techniques, with a suite of technical challenges related to the type and quality of the data. The data available in this thesis consisted of a series of environmental variables from different sources that had to be scaled to a standard grid. A loss of important local information likely resulted from this process. Furthermore, the expected finding of spatial autocorrelation led to a methodology that produced simple models, mostly made up of only two variables.

The purpose of this thesis was to explore the utility of logistic regression for the projection of habitat suitability for the thirteen species of Spanish snakes under a climate change scenario. In this exercise the current distributions of the snakes were related to a set of 18 climate and topography predictors. The results obtained allowed classification of the Spanish snakes into four classes: species widely distributed, not amenable to modelled; species widely distributed in the Mediterranean region, not amenable to be modelled; Eurosiberian species limited by precipitation; and Mediterranean species limited by temperature.

The implementation of the Hadley scenario into the logistic models illustrated the magnitude of effects that might be expected as a consequence of climate change. From this physiographic approach, *Coronella austriaca*, *Coluber viridiflavus* and *Elaphe longissima* face entirely or almost entirely unsuitable conditions for persistence. *Hemorrhhois hippocrepi*, *Macroprotodon brevis* and *Vipera seoanei*, might experience drastic extirpations and fragmentations of their current distributional areas and might extend their distributions to new areas. Finally, *Vipera aspis* might be particularly favoured by the projected effects of global warming.

Based on different model performance measurements, logistic regression produced relatively valid results. However, in some cases these measurements did not match the visual assessments of the outcome maps. From a series of potential statistics for evaluating model performance, the R^2 proved to be the most reliable measurement, except for the most narrowly distributed species for which no index seemed appropriate. From this point of view, the most reliable models might be those with higher R^2 and derived from species with a minimum number of cells in which the species is currently present. Rodríguez (pers. comm.) suggested that to produce a credible model one needs at least 5 % of all grids containing the species. Only the model for *Vipera seoanei* fulfilled these two conditions (high R^2 and enough number of presences) and therefore might be reasonably credible. The reliability of the remaining models might decrease as the current number of presences and the R^2 decrease. For these models, only the general positive or negative effects of climate change might be judged. Consequently, the overall result is that of increasing tendency for species extirpation. In this respect, this thesis may assist to alert the public, conservation planners and other professionals to the potential negative

impact of climate change to the natural world and to bring home the message of the need for urgent reduction in greenhouse gas emissions (Teixeira and Arntzen, 2002).

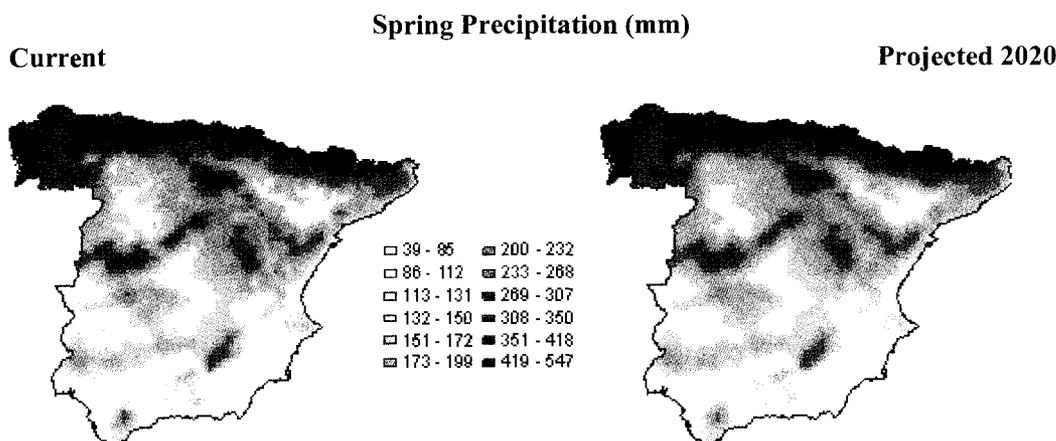
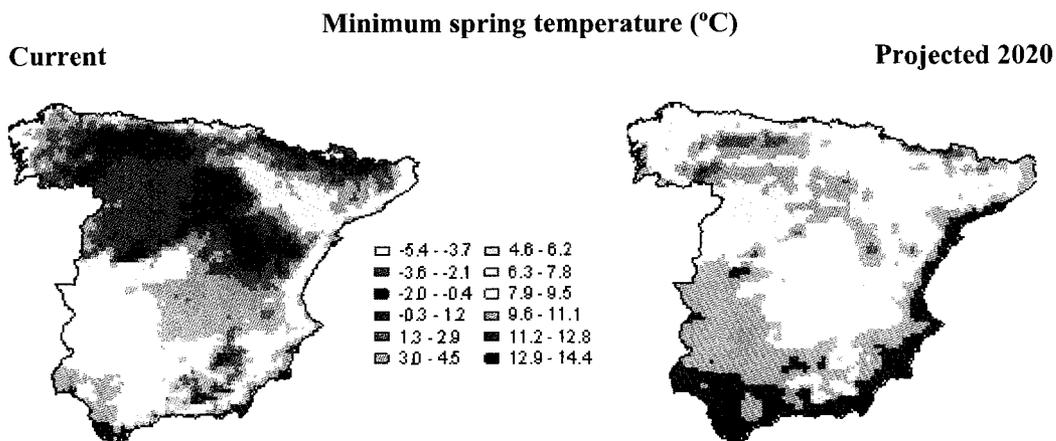
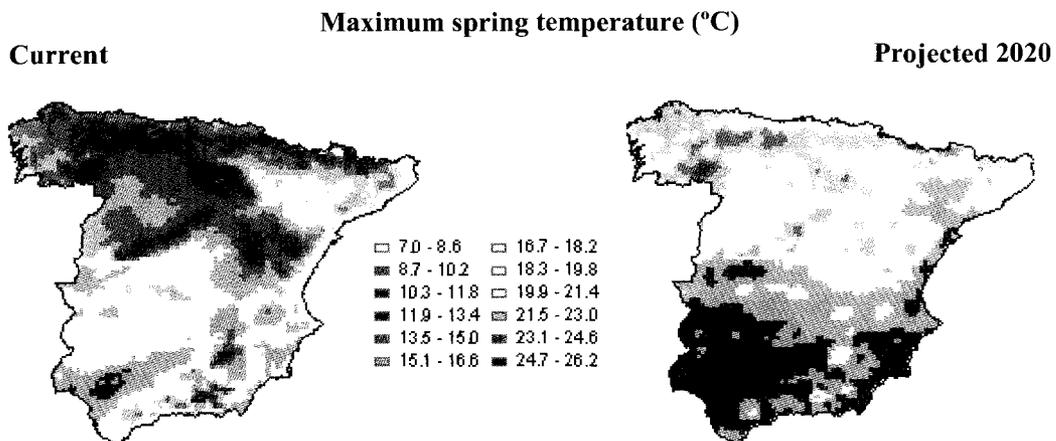
Because any model is a simplification of a biological system, it cannot be perfectly predictive. Hence, as Horne (2002) pointed out, a model may be seen as a hypothesis that we know is not true, but we may choose to keep because it is useful. Consequently, the models produced in this thesis may not be perfectly true but may help Spanish conservation managers in the identification of responses of Spanish snakes to climate change, detection of future endangered areas, and towards the development of habitat corridors that may allow dispersal to areas that will become suitable in the near future.

In the future, a similar study might be done at a European scale where we might reasonably expect that, with a much wider range of climates, we could find that the snakes which seemed not to be sensitive to climatic differences within Spain would find that their limits elsewhere within Europe would be influenced by climate patterns.

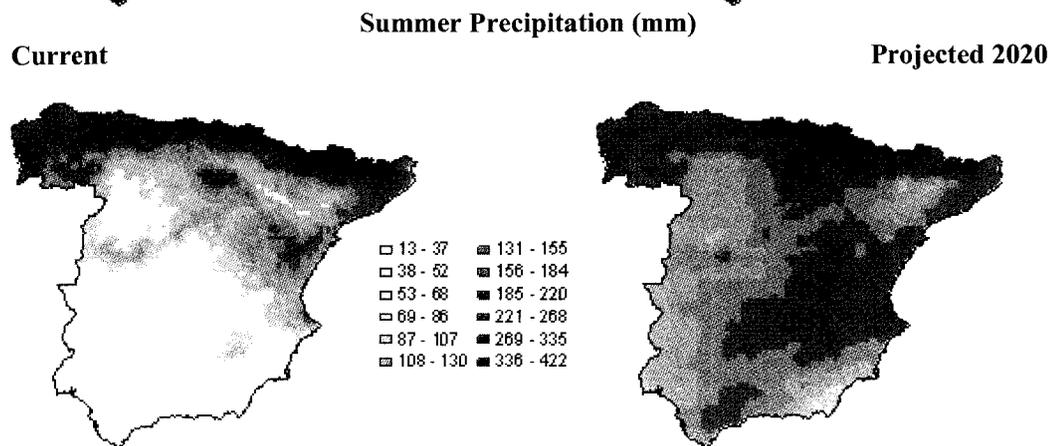
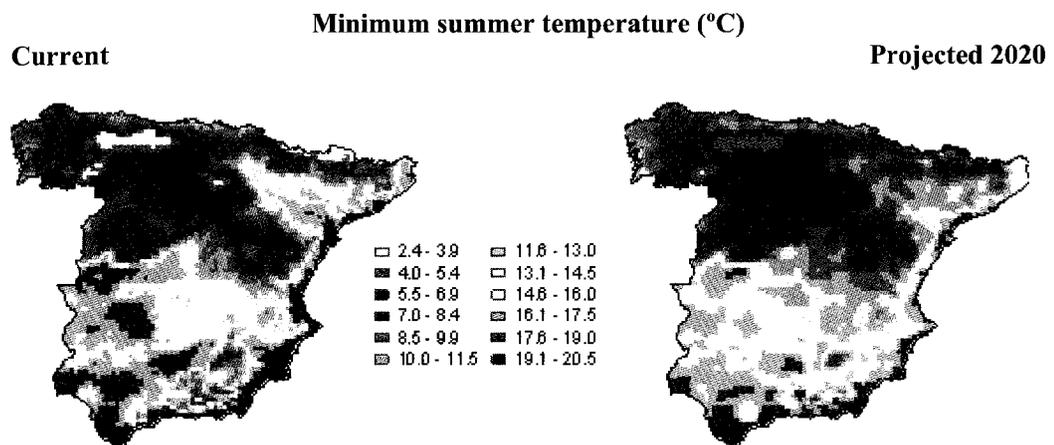
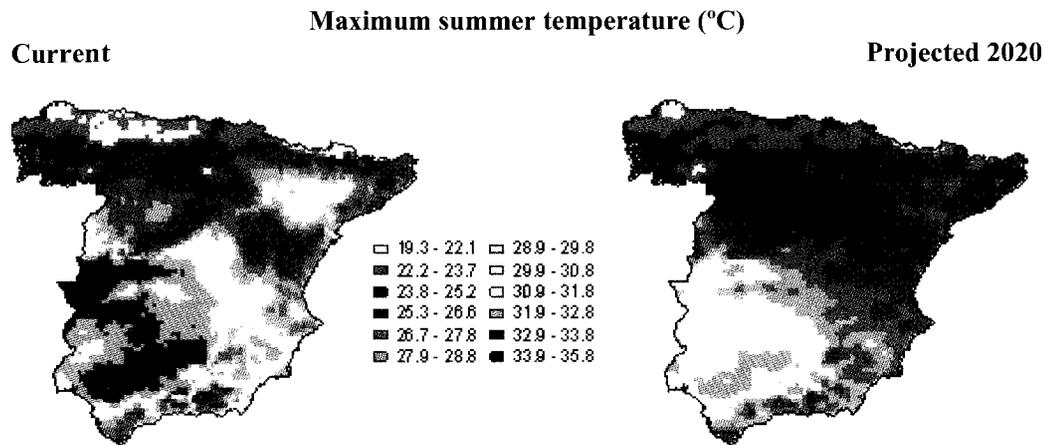
Furthermore, the potential current distribution derived from the models showed some areas where the species are not currently present but indeed, according to the models are suitable for their survival. The species could already be present in these areas but not prospected or they may be absent because factors other than climate and topography may be preventing the species from living in these regions. New sampling campaigns could be focused on these areas in order to determine if existing populations were missed. In addition, differences in habitats between the original distributional areas of the species and the potential current distribution modelled areas could be recorded in order to find which other factors are affecting the species survival.

In summary, at least four sources of uncertainties are inherent to the modelling process presented in the current research (Thuiller, 2003): the uncertainty associated to the climate change scenario, the uncertainty based on the reliability of the presence/absence data, the uncertainty associated to the preparation of the data and the uncertainty based on the modelling technique. Thus, other modelling techniques and other climate change scenarios should be assessed and compared with the current approximation. Because there is considerable uncertainty as to the actual extent of climate change, running models with different scenarios would provide a range of outcomes as well as a more complete understanding of the uncertainty surrounding the response snakes to the climate change (Matthews et al., 2004). Because there is also uncertainty related to the logistic regression (especially for the more restricted species) projections of future potential distributions might be carried out using a variety of modelling techniques to draw conclusions by comparisons among outputs. These conclusions and validations could be based on expert knowledge or published studies (Thuiller, 2003).

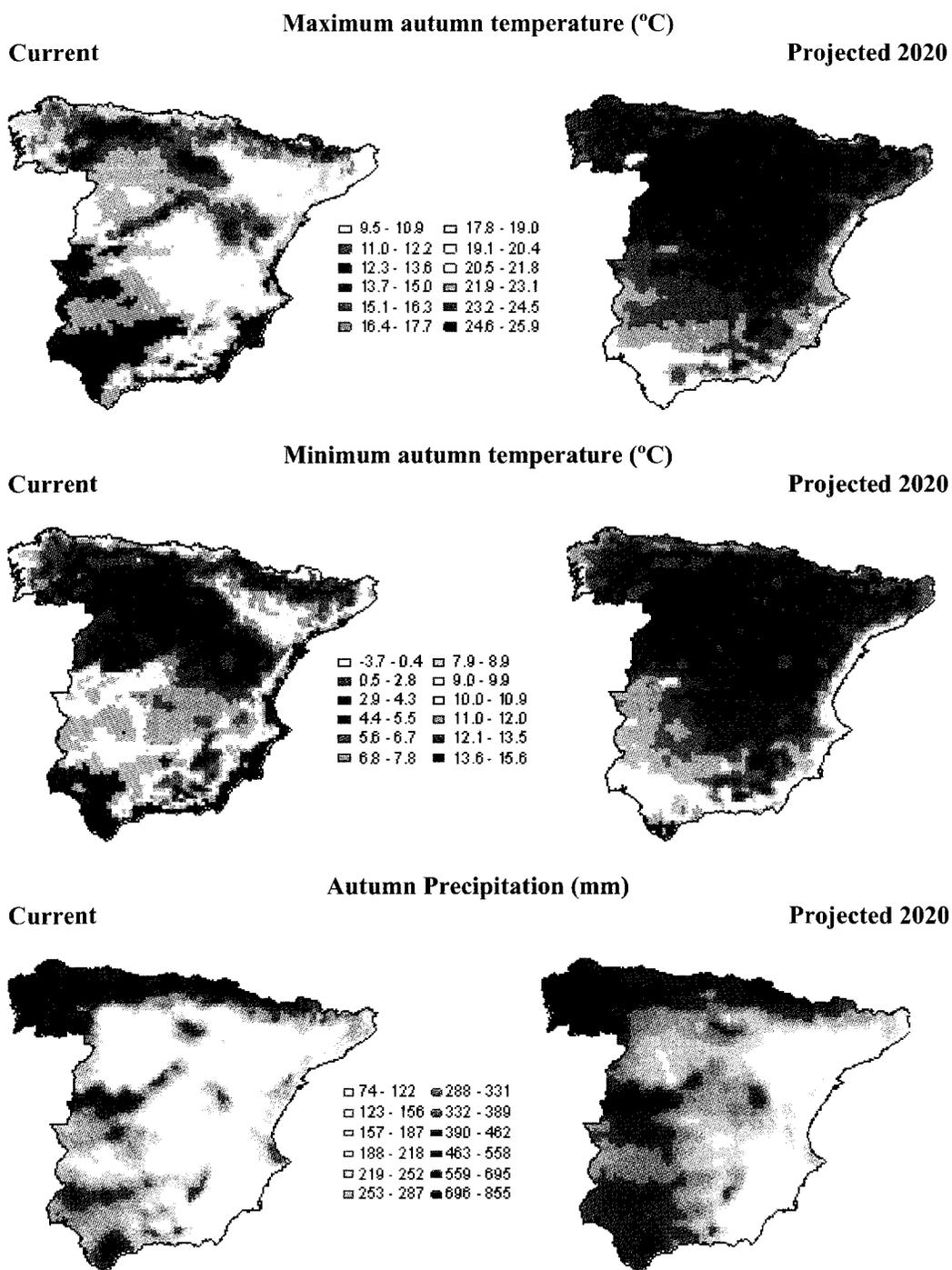
APPENDIX 2: Current and future projections for Spring Maximum and Minimum Temperature, and Precipitation in the Spanish Iberian Peninsula.



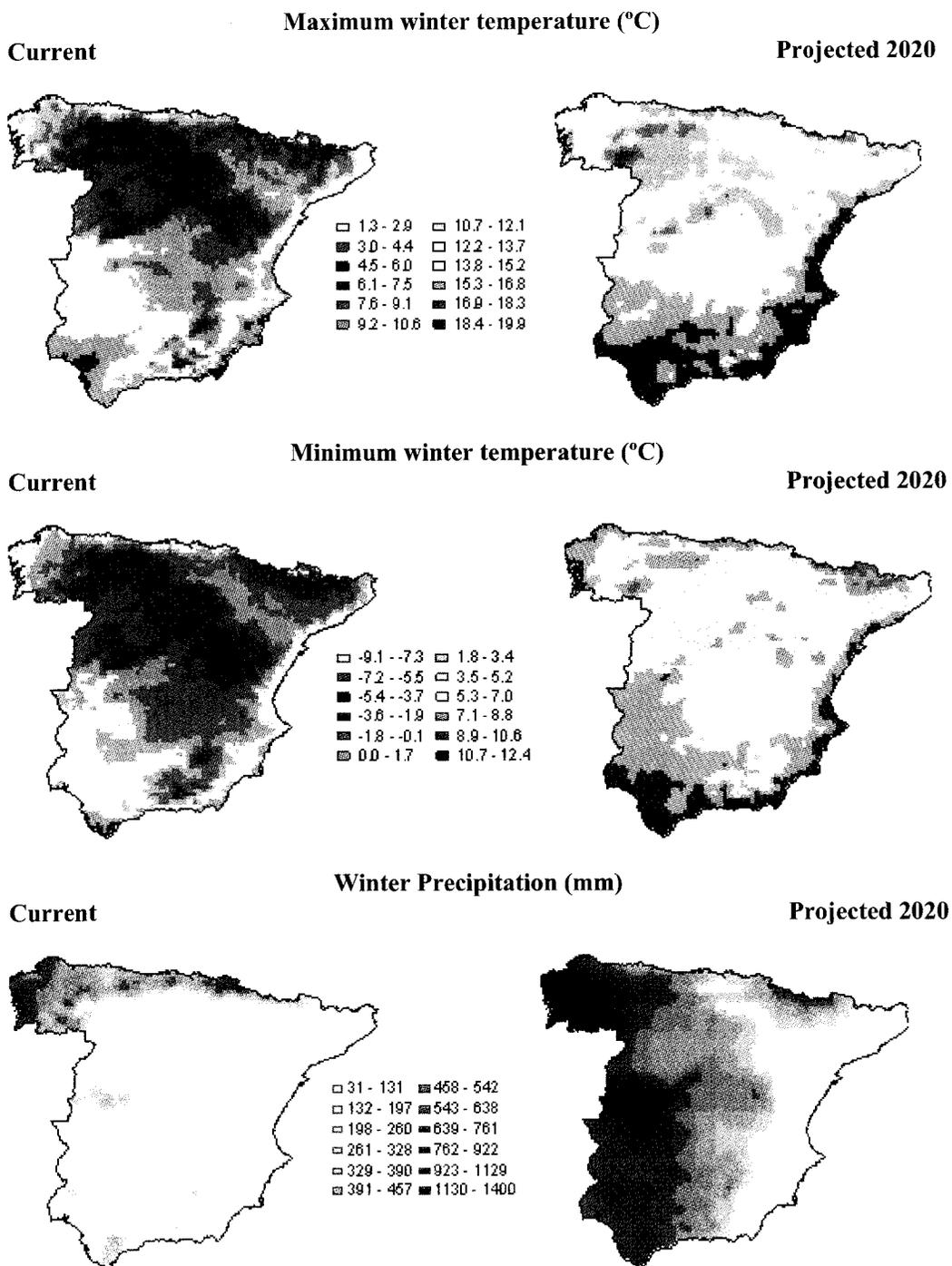
APPENDIX 3: Current and future projections for Summer Maximum and Minimum Temperature, and Precipitation in the Spanish Iberian Peninsula.



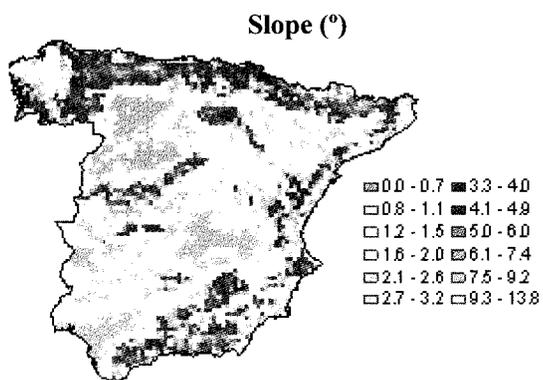
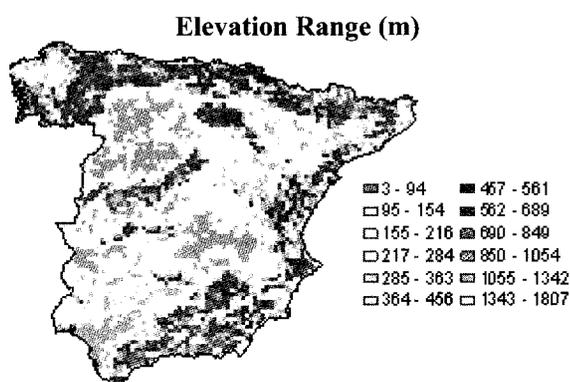
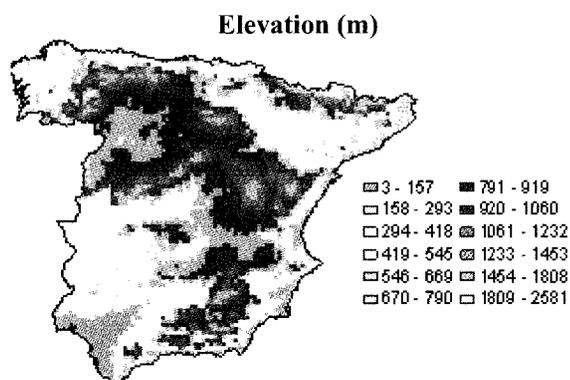
APPENDIX 4: Current and future projections for Autumn Maximum and Minimum Temperature, and Precipitation in the Spanish Iberian Peninsula.



APPENDIX 5: Current and future projections for Winter Maximum and Minimum Temperature, and Precipitation in the Spanish Iberian Peninsula.



APPENDIX 6: Elevation, Elevation Range and Slope in the Spanish Iberian Peninsula.



APENDIX 7: Spanish climate change scenario comparison

To test the consistency of the scenario applied in the current research it was compared with the study from Hulme and Sheard (1999) where annual temperature and annual precipitation in 2020 was projected in the Iberian Peninsula. Hulme and Sheard (1999) divided the Iberian Peninsula into 8 gridboxes, leaving aside the southeast part of Spain. In order to compare, the current research's standard grid was divided into gridboxes equivalents to the ones used by Hulme and Sheard (1999) (Figure A7.1).

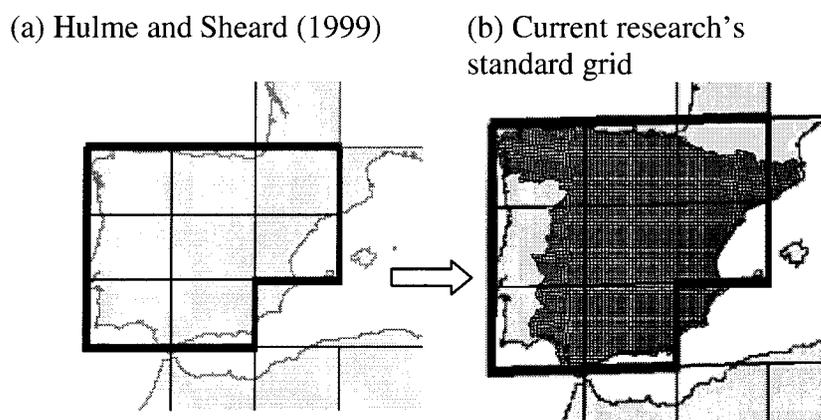


Figure A7.1: Grid used in Hulme and Sheard (1999) (left). The standard grid used in the current research was matched into the Hulme and Shepard grid's to compare climate change outputs.

2020 Temperature (°C)

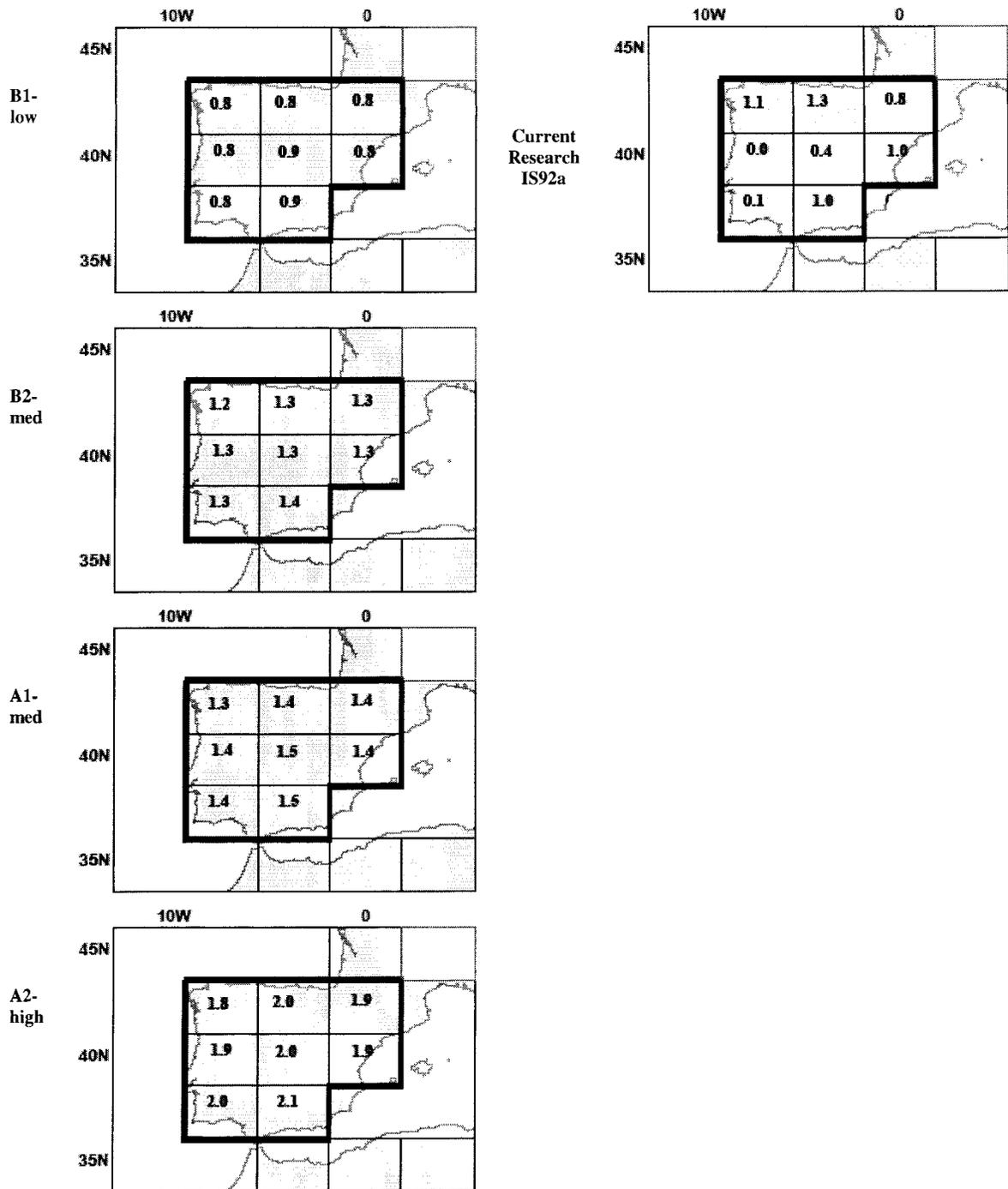


Figure A7.2: Change in mean annual temperature in degrees Celsius from the average 1961-90 in Hulme and Sheard (1999) study (left) and 1971-2000 in my study (right) respect to the 2020 value. The printed numbers show the estimated change for each model land gridbox. over Iberia (Adapted from Hulme and Sheard, 1999).

2020 Precipitation (%)

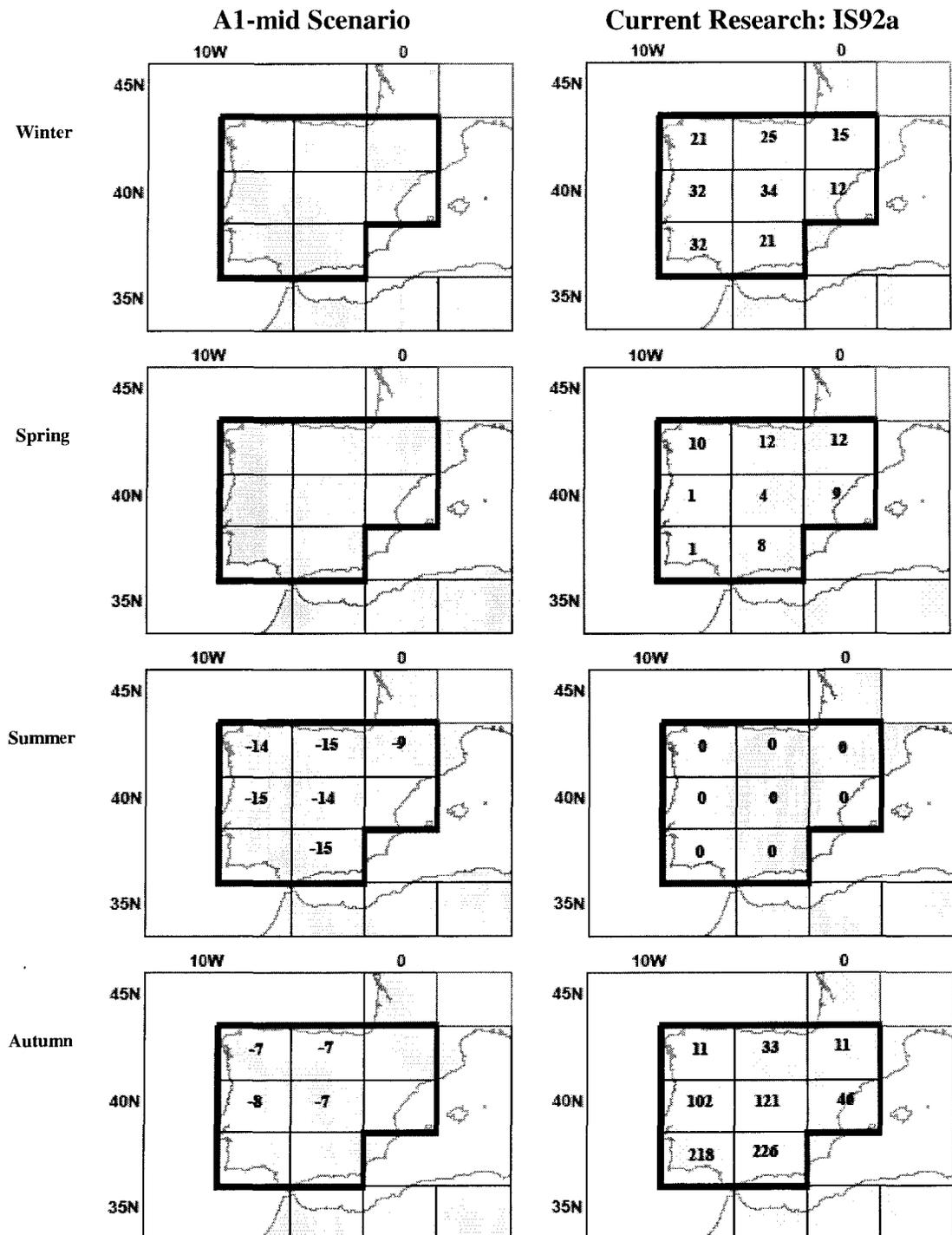


Figure A7.3: Change in mean annual precipitation in percentage from the average 1961-90 in Hulme and Sheard (1999) study (left) and 1971-2000 in my study (right) respect to the 2020 value. The printed numbers show the estimated change for each model land gridbox, over Iberia. In Hulme and Sheard (1999), changes were only shown where they were large in relation to natural precipitation variability on 30-year timescales. (Adapted from Hulme and Sheard, 1999).

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