



# El Mirón Cave, Cantabrian Spain

**The Site and Its Holocene Archaeological Record**

EDITED BY  
**LAWRENCE GUY STRAUS AND  
MANUEL R. GONZÁLEZ MORALES**

# The Holocene Herpetofauna of El Mirón Cave

Borja Sanchiz, Jorge M. Lobo, and Salvador Bailon

TRANSLATED BY LAWRENCE GUY STRAUS

---

The excavations directed by M. González Morales and L.G. Straus in El Mirón Cave yielded relatively few remains of amphibians and reptiles from the Holocene deposits. These are the subject of the present zooarchaeological analysis, complementing the studies of other zoological groups reported upon in this monograph. González Morales and Straus (2000a, b; Straus et al. 2001) provide the relevant details about the site and its stratigraphy, archaeology, and chronology.

## Methods

### TAXONOMIC IDENTIFICATION

The taxonomic nomenclature used here follows Salvador (1998) and Frost (2010). The morphological traits used for identification are based on the criteria developed by Bailon (1999) and Böhme (1977) for the anurans and Szyndlar (1984) for the ophidians, as well as on direct comparisons with material in the collections of the Museo Nacional de Ciencias Naturales (CSIC) in Madrid.

### ARCHAEOZOOLOGICAL CRITERIA

The calculation of minimum numbers of individuals (MNI) is based on the most numerous single skeletal element per species from each stratigraphic level, taking into account side as well as sex in cases of clear sexual dimorphism.

### BIOLOGICAL INFORMATION

The information that we provide on ecological aspects of the species (periods of activity, predators, etc.) is taken from works by Barbadillo et al. (1999), Salvador (1998), Salvador and García-París (2001), and Salvador and Pleguezuelos (2002). All the species represented in the early to mid-Holocene levels of El Mirón are found today in Europe. For their

continental distributions, one can consult Gasc et al. (1997). The syntheses of Holman (1998) and Martín and Sanchiz (2010) provide data on the presence of these taxa in other European Quaternary sites.

#### BIOGEOGRAPHICAL CRITERIA

Information on modern species's geographical ranges is taken from the recent herpetological atlas of Spain (Pleguezuelos, Márquez, and Lizana 2002), which was done on a UTM projection with a resolution of 10 × 10 km cells. We selected as our study area those 100 km<sup>2</sup> cells within the Iberian northern Atlantic climatic zone (with the exclusion of small portions of northern Portugal, for which adequate information is lacking).

The geographic analysis was done using the IDRISI 32 GIS software (Eastman 2001). For each 100 km<sup>2</sup> grid we included the following information: (1) climatic data (average annual temperature, total annual precipitation, and annual insolation) as provided by the Spanish Instituto Nacional de Meteorología, (2) altitudinal data (average elevation) according to a digital terrain model (Clark Labs 2000) with a resolution of 1 km, (3) data on groundcover and land use (woods, brush or heathlands, cultivated fields, pastures) according to the CORINE Land Cover 2000 Project database (freely available at <http://terrestrial.eionet.europa.eu/CLC2000>) and (4) lithological data (siliceous or calcareous soils) derived from the Spanish national soils atlas (ITGE 1988). The data on lithology and groundcover/land use were transformed into qualitative variables that represent the presence or absence of high percentages (>75% of land area) of each category.

Following the methodology detailed in Sanchiz and Lobo (2006), we develop probabilistic models for species distributions using the Biomapper 2.1 program (Hirzel et al. 2002). To do this, we calculate a series of uncorrelated environmental factors that summarize the main environmental gradients that exist in the region. These factors allow us to generate a map (or maps) of environmental suitability for each species by means of a comparison of the general values from the region with those that occur in the cells in which each species or group of species is actually present. One can thus estimate how probable it is that any particular place belongs to the environmental domain of those places in which the presence of a particular species (or group of species) has been ascertained.

This methodology is an alternative to the climatic inferences exclusively based on the observed occurrences of a species, as recently done for the Pleistocene (e.g., Blain, Bailon, and Cuenca-Bescós 2008; Blain et al. 2009) and tries to skip the nonrandom prospection in the making of herpetological distribution atlases.

The variables selected for making paleoclimatic inferences are: (1) annual average temperature (°C), (2) annual precipitation (mm), (3) annual insolation (hours of sunlight), and (4) altitude (m). The last variable, whose value obviously has not changed for the site during the Holocene, acts in fact in zoogeography as a resultant factor that incorporates several occult populational variables, such as longevity or growth rate (see, e.g., Esteban and Sanchiz 2000).

The species selected for biogeographic analysis were *Anguis fragilis*, *Bufo bufo*, and *Rana temporaria*, in two different combinations representative of the herpetofaunas from most of the levels. The remains of other species are sporadic, and their absences from some of the levels are not statistically significant. The environmental conditions of the grids showing the joint presence of a selected group of species are compared with those for which these species have not been cited. We also compare the environmental values for those zones with high and low probability of presence of the above-mentioned species groups, according to their predictive models of habitat suitability. These calculations were done with Statistica 6.1 software (StatSoft Inc. 2003).

#### Material

The Holocene herpetological material is stored in the Museo de Prehistoria y Arqueología de Cantabria, Santander. It consists of 356 bone fragments, of which 331 could be identified to species or genus level. The distribution of the finds by taxa and levels is presented in table 14.1. All remains seem to belong to adult individuals.

#### Results

##### PALEONTOLOGICAL ANALYSIS AND ECOLOGICAL AND TAPHONOMIC OBSERVATIONS

UTM grid cell VN69, where El Mirón Cave is located, has been at present relatively little surveyed for herpetofauna (only 6–10 citations, according to Pérez-Mellado

and Cortázar [2002]). As a result, the national atlas (Pleguezuelos, Márquez, and Lizana 2002) lists only the documented presence of common wall lizard (*Podarcis muralis*) and Iberian adder (*Vipera seoanei*) in this grid. However, many of the (apparent) absences are presumably due to sampling deficiencies, and in fact all the species found in the archaeological site are present today in nearby grids. The species identified in the site are as follow:

### Family Salamandridae

*Salamandra* (Garsault, 1764)

*Salamandra salamandra* (Linnaeus, 1758)

A single vertebra from Level 8 attests to the presence of the fire salamander at the site in late Neolithic times. On the Iberian Peninsula this is a polytypic species, with several subspecies that are very diverse in terms of morphology, reproduction, and autoecology. In general, these are animals characteristic of areas with high humidity, abundant in the Cantabrian region in deciduous forests. It is a nocturnal species that is inactive at temperatures <3°C. Its annual period of activity is highly variable; depending on local conditions, it can be active from February to March and October to November, with a period of hibernation, or even all year except for a period of aestivation in summer. Thus this species can provide no archaeozoological information on seasonality.

Several reptiles (*Natrix natrix*, *Vipera seoanei*), birds (*Buteo buteo*, *Strix aluco*, and *Turdus torquatus* but never *Tyto alba*) and mammals (*Lutra lutra*, *Meles meles*, *Sus scrofa*) are known predators of adult *Salamandra salamandra*. Such predation is, however, rare in nature, since the fire salamander has a conspicuous aposematic coloration and secretion glands that produce a strong neurotoxic alkaloid.

### Family Alytidae

*Alytes* (Wagler, 1830)

*Alytes obstetricans* (Laurenti, 1768)

The common midwife toad is currently diversified into several subspecies on the Iberian Peninsula. The European form, *A. o. obstetricans*, is present in Asturias, Cantabria, Basque Country, and Navarra. However, it is not possible to identify the available archaeofaunal

material to the subspecific level. This species is found in a wide variety of habitats. It is active at dusk and during part of the night, although it can also be seen during the day under cloudy, humid conditions. Its annual period of activity is restricted to the months between February and November, with a short period of hibernation. Adults are predated by snakes (*Natrix natrix*, *Natrix maura*, *Vipera seoanei*), birds (*Lanius excubitor*, *Strix aluco*, *Tyto alba*), and carnivores. In the case of *Tyto alba*, the owl pellet collection of J.M. Rey (Universidad de Santiago de Compostela) contains 16 places where *A. obstetricans* was hunted by the barn owl, making up about 1.5 percent of the prey among the lots in which this amphibian is found. These findspots are in Alava, northern Burgos, Cantabria, and Vizcaya. Judging by the periods in which the barn owl hunted this toad, the annual maxima clearly correspond to the periods of March–April and July–August, which is an indirect indicator of the times during which the midwife toad is more active and conspicuous (and thus available for predation) in this region.

### Family Bufonidae

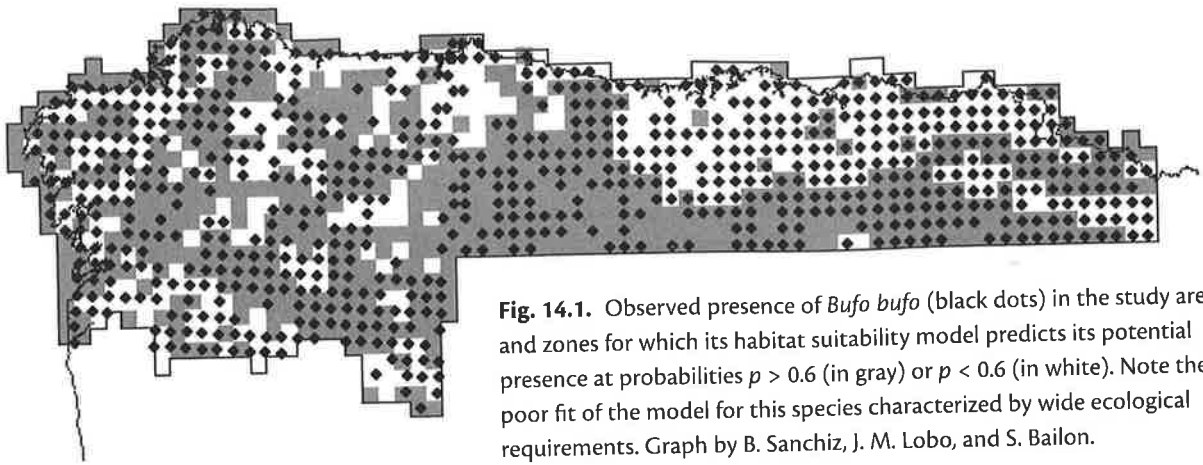
*Bufo* (Garsault, 1764)

*Bufo bufo* (Linnaeus, 1758)

The common toad is one of the most frequently represented amphibian species in European archaeological sites. Unfortunately the lack of osteometric studies of living populations makes it impossible to identify the subspecies found in El Mirón, there being currently at least three reasonably differentiated subspecies on the Iberian Peninsula (Lizana 2002).

The wide variety of environmental conditions under which *Bufo bufo* lives in its very broad distribution throughout Europe means that as a species it is a poor environmental indicator (figure 14.1). In the study region the common toad always has a period of hibernation, being active mostly between March and October, although sporadically it can also be seen outside of this period, depending on local circumstances. It is occasionally the prey of a great number of species, from snakes (*Natrix natrix*), diurnal birds, and nocturnal raptorial birds (*Bubo bubo*, and *Strix aluco*, but not *Tyto alba*) to mammals (e.g., *Lutra lutra*, *Meles meles*, *Mustela putorius*, *Sus scrofa*, *Vulpes vulpes*). In the case of El Mirón Cave, the predators could have belonged to the last two





**Fig. 14.1.** Observed presence of *Bufo bufo* (black dots) in the study area and zones for which its habitat suitability model predicts its potential presence at probabilities  $p > 0.6$  (in gray) or  $p < 0.6$  (in white). Note the poor fit of the model for this species characterized by wide ecological requirements. Graph by B. Sanchiz, J. M. Lobo, and S. Bailon.

groups, judging from the fragmentation of the toad bones and traces of digestion, as described by Pinto Llona and Andrews (1999).

#### Family Ranidae

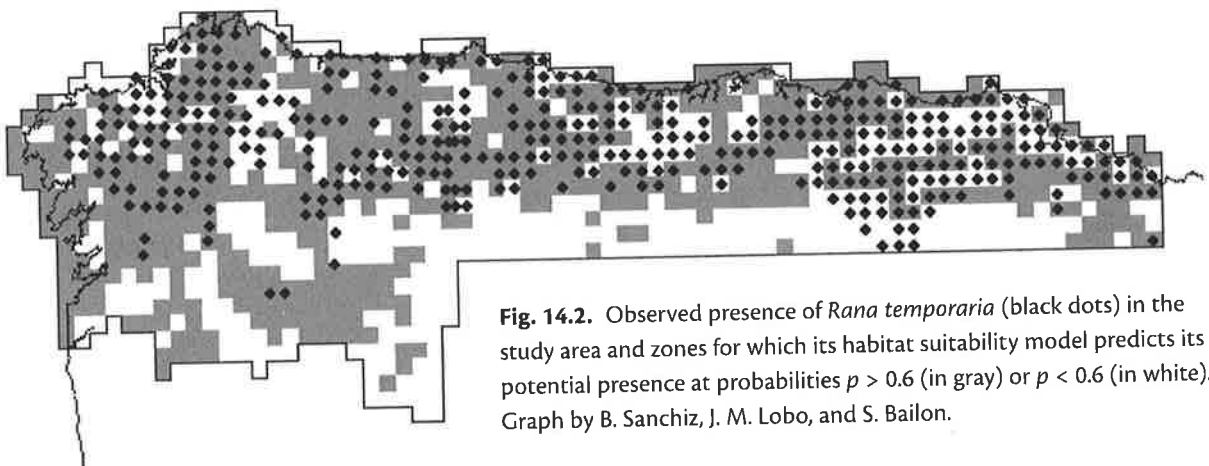
*Rana* (Linnaeus, 1758)

*Rana temporaria* (Linnaeus, 1758)

The grass frog is without doubt the amphibian species most commonly found in Quaternary sites in Atlantic Europe. Today it is widely distributed throughout all of non-Mediterranean Europe, even reaching northern Scandinavia (Gasc et al. 1997). On the Iberian Peninsula, the southern limit of its distribution lies precisely in the study region, for which reason we could expect that at the El Mirón site it should behave as a fairly sensitive

environmental indicator at the extreme edge of its ecological range (figure 14.2).

The period of activity of *R. temporaria* throughout the year is highly variable. Hibernation is a requirement that is both ecological and physiological for this species. It has been demonstrated experimentally that gametogenesis requires a temperature below 6–7°C during two or more weeks for maturation. Thus the distribution of the species, according to Balcells (1975), approximately fits the 5°C isotherm for average January temperature. Like other anurans, the grass frog is generally nocturnal in its habits. Its period of reproduction can even include some days in December or January, but the time when adults are at greatest risk of being killed by predators of archaeological interest (such as the barn owl) seems to be between April and September. Thus attests J. M.



**Fig. 14.2.** Observed presence of *Rana temporaria* (black dots) in the study area and zones for which its habitat suitability model predicts its potential presence at probabilities  $p > 0.6$  (in gray) or  $p < 0.6$  (in white). Graph by B. Sanchiz, J. M. Lobo, and S. Bailon.

Rey's barn owl pellet collection at the Universidad de Santiago, in which there are 14 findspots in Cantabria with remains of grass frog kills that occurred during this period, with a maximum in July.

Known predators of *R. temporaria* include some snakes (particularly during mating season), occasionally diurnal birds and mammals, and especially nocturnal raptorial birds. In the El Mirón case, and following the criteria given by Pinto Lloná and Andrews (1999), a large part of the material seems to have come from barn owl pellets, but there are also clearly some bones that, because of their types of breakage and digestion traces, must be attributed to predation by other owls and perhaps even by mammals. Some of the remains present a characteristic kind of alteration in the form of deep arabesque etchings that might be attributed to small rootlets (Y. Fernández-Jalvo, pers. comm., 2003).

#### Anura indet

This group includes poorly preserved fragments that most likely belong to either *Bufo bufo* or *Rana temporaria*. In the samples that we have studied there is no evidence of any amphibian species different from the ones already mentioned above.

#### Family Anguillidae

*Anguis* (Linnaeus, 1758)

*Anguis fragilis* (Linnaeus, 1758)

The slow worm usually buries among dead leaves or under stones, superficially digging in loose soils, but it is not considered able to contaminate deep strata. This

species is active between March and October and is nocturnal (or crepuscular) in its habits. Among its known predators are (sporadically) certain snakes (*Vipera seoanei*), birds of prey (e.g., *Buteo buteo*, *Strix aluco*), and mammals (*Lutra lutra*, *Martes martes*, *Meles meles*, *Sus scrofa*, *Vulpes vulpes*). We cannot determine the taphonomic origin of the slow worm remains in El Mirón (figure 14.3).

#### Family Colubridae

*Coronella* (Laurenti, 1768)

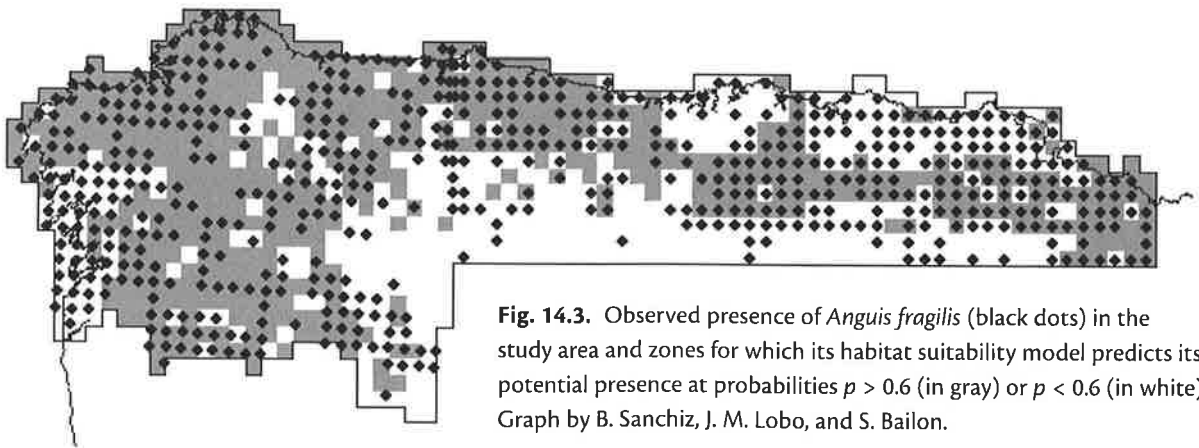
*Coronella* sp.

The only two remains of this genus (found in Levels 3.5 and 10.1) cannot be securely identified to the species level. However, they might very possibly pertain to the smooth snake (*Coronella austriaca*), a species that is common in Europe and is present in the Eurosiberian region of the Iberian Peninsula, where it inhabits humid areas with annual precipitation over 600–800 mm (Pleguezuelos, Márquez, and Lizana 2002). The two European species of this genus (*C. austriaca* and *C. girondica*) are active between March and October.

*Zanemys* (Wagler, 1830)

cf. *Zanemys longissimus* (Laurenti, 1768)

The only fragment of this genus (from Level 4) possibly belongs to the Aesculapian snake (*Z. longissimus*), since the only other similar Iberian species (*Rhinechis scalaris*) is a Mediterranean form that does not currently live in the Cantabrian region (Pleguezuelos and



**Fig. 14.3.** Observed presence of *Anguis fragilis* (black dots) in the study area and zones for which its habitat suitability model predicts its potential presence at probabilities  $p > 0.6$  (in gray) or  $p < 0.6$  (in white). Graph by B. Sanchiz, J. M. Lobo, and S. Bailon.

Honrubia 2002). However, this identification cannot be confirmed morphologically. These two species were previously included in the genera *Elaphe* and exhibit a close vertebral morphology.

*Natrix* (Laurenti, 1768)

*Natrix natrix* (Linnaeus, 1758)

The grass snake is a basically diurnal species that is active mainly between March and October (Braña 1998). It is prey to diurnal raptorial birds (e.g., *Circaetus gallicus*, *Milvus milvus*, *M. migrans*) and mammals (e.g., *Lutra lutra*, *Martes foina*, *Meles meles*).

*Natrix* sp.

It is very possible that all this material may also pertain to the grass snake (*N. natrix*), although it cannot be unequivocally identified to the specific level.

### Family Viperidae

*Vipera* (Laurenti, 1768)

*Vipera* sp.

There is only one bone (a vertebral fragment from Level 9.6) that attests to the presence of the viper at this site, although it is not clearly identifiable to the species level. At the present time there are two species that live together in part of Cantabria: *Vipera aspis* and *V. seoanei* (although they may not be strictly syntopic). This region also borders to the south with the distribution of *V. latasti*; thus a fairly short radius around the site may include the range of all three of the Peninsular vipers (Pleguezuelos, Márquez, and Lizana 2002). All the Iberian species of *Vipera* are diurnal and active between April and October.

### ABSENT SPECIES

Negative evidence is rarely admissible in paleontological studies. In this case, however, it is worthwhile to note that we have found no remains of *Discoglossus galganoi*. Among the anurans, this species is consumed by *Tyto alba* relatively often (similarly to *Rana temporaria*). *D. galganoi* has been found at present in at least 11 barn owl pellet spots in Cantabria (J. M. Rey, pers. comm., 2003). Given that this owl was probably the

agent of accumulation for most of the remains of *Rana temporaria* in the Holocene deposits of El Mirón Cave, it would be logical to detect the presence of *D. galganoi* in these archaeofaunal assemblages if it had been living in the region at the time. It can thus be supposed that this species has been expanding eastward along the Cantabrian region during the Holocene and that it had not reached the Río Asón drainage basin by Bronze Age times. Similar reasoning was used (Sanchiz 1980) in the case of La Paloma Cave in central Asturias, 200 km west of El Mirón. The barn owl today preys in situ at La Paloma on this species, which, however, does not appear in the most recent levels studied in the archaeological site, namely the Magdalenian and Azilian.

### TAPHONOMIC NOTES AND INTER-LEVEL COMPARISONS

The above-mentioned annual periods of species activity would seem to indicate that death and subsequent burial of the herpetofaunal remains took place essentially between the months of March and October. All the remains seem to have been the result of animal predation, there being no evidence of human interaction with the herpetofauna.

The small sample size makes it difficult to be sure whether the inter-level differences among identified herpetofaunas are real or not. In the case of the sporadic trace appearances of *Salamandra salamandra*, *Alytes obstetricans*, and the ophidians (table 14.1), it is impossible to establish faunal comparisons. The grass frog, on the contrary, appears in all the Holocene levels. Assuming theoretically (but perhaps not very realistically) that the taphonomic processes acting on the herpetofauna had remained the same among the levels, one could determine whether the absences of *Bufo bufo* and *Anguis fragilis* in any given level are genuine and not simply accidents of sampling. The results of such a statistical determination are, however, not clear in our case, since a chi-square analysis on *Bufo bufo* shows that the expected proportion of minimum numbers of individuals does not differ significantly from the observed MNI. This could point to some possibly true absences. However, in terms of number of identified bones, there is a significant difference ( $p < 0.001$ ). For *Anguis fragilis* the statistical results are the reverse, although in this species the tiny size of the remains could have affected

collection, thereby causing a biased impression of (false) species absences. Given all this, we have opted in the eco-geographic section of this chapter to separately analyze two faunal assemblages that cover almost all the excavated levels. These are, on the one hand, the group made up of *Bufo bufo* + *Rana temporaria* (B+R group) and, on the other hand, the group of *Anguis fragilis* + *Bufo bufo* + *Rana temporaria* (A+B+R group).

#### ZOOGEOGRAPHIC AND PALEOCLIMATIC ANALYSES

The geographic distribution of amphibians and reptiles, given their ectothermic (cold-blooded) metabolism, is heavily conditioned by environmental factors. For this reason, quantitative biogeographic analysis is of great potential archaeozoological interest. In the present case there are limitations deriving mainly from the information provided by distributional atlases. First, the best resolution (Pleguezuelos, Márquez, and Lizana 2002) is the 10 × 10 km UTM grid. This means that each spatial unit is defined by the *average* of the different local values present, which might be quite diverse in a mountainous area. Second, the atlas provides indications about species “presence” or “absence,” but it is a virtually certain fact that there are grids with false absences due to incomplete prospection.

The species that we have selected as environmental indicators (*Anguis fragilis*, *Bufo bufo*, and *Rana temporaria*) are easy to find in a survey campaign, a fact that minimizes the “false absence” problem. However, we preferred the strategy of making predictive maps of habitat suitability, based exclusively on verified presences and on global conditions within the study zone—that is, on positive evidence. Figures 14.1–14.3 display the individual cases of *Bufo bufo*, *Rana temporaria*, and *Anguis fragilis*, respectively.

These probabilistic maps can also be made for groups of species, such as our B+R group (places where *Bufo bufo* and *Rana temporaria* potentially coexist) and our A+B+R group (where the former two species can live together with *Anguis fragilis*). These maps can give us a first estimate of the most probable paleoenvironmental conditions. Next we statistically compare the environmental conditions among the places with high and low probabilities of being ideal for these herpetological groups and, in the event that the results are significant, we establish their confidence intervals.

The results of the analysis of the potential joint distribution model for group B+R (from Sanchiz and Lobo, 2006) and group A+B+R, created as if they were virtual single taxa, are presented in table 14.1. The values inferred for B+R indicate that the insolation factor does not differ between places with low and high habitat suitability for this group. However, both the precipitation and altitude factors are significantly greater in the more suitable grids for the joint presence of these two amphibians, while, to the contrary, the temperature factor is lower. In the case of the A+B+R group altitude does not yield significant differences, but precipitation (much greater in the more suitable zones) and temperature and insolation (both smaller in the most suitable zones) do show significant differences.

Table 14.2 shows the confidence intervals of these variables for the habitat suitability analysis as well as their current values in the 10 × 10 km UTM cell corresponding to the El Mirón location.

The provided results show that modern values for precipitation and temperature in the UTM grid cell VN69 lie outside the 95 percent confidence interval of a normal distribution for these variables in the zones whose potential habitat suitability is high, with respect to both faunal groups, B+R and A+B+R (table 14.3). This situation also obtains—albeit at a more marginal level—in the case of the insolation factor for group A+B+R.

If the habitat suitability values inferred for the El Mirón area may be extrapolated to past conditions, these results would allow us to deduce that, for practically all the levels with studied herpetofauna, early to mid-Holocene climatic conditions at the cave were significantly colder and drier than those of the present. The method of numeric biogeography also permits quantification of this paleoenvironmental inference. In this case it assigns annual precipitation values that are never above 1,192 mm for levels with the B+R group or never above 1,303 mm for levels with the A+B+R group and average annual temperatures never above 10.8°C for levels with the B+R group or 11°C for levels with the A+B+R group.

These results are congruent with information derived from the other vertebrates (birds and mammals) from the site (as reported by Elorza [chap. 13], Cuenca Bescós and García Pimienta [chap. 12], and Altuna and Mariezkurrena [chap. 16], this volume). They amount



to one more confirmation of the prevailing paleoenvironmental scheme for northern Spain, according to which this area of Cantabria has never been outside of the Eurosiberian biogeographic zone during the course of the Holocene. In fact, it is for the present time that the herpetofaunal data show the highest levels of temperature and precipitation for this area—the closest ever during isotope stage 1 to the Mediterranean biogeographical province.

The scarcity of remains and the low species diversity in the sample that we have been able to identify from the Holocene deposits excavated in El Mirón Cave do not allow for more precise ecogeographic analyses, but their comparison with the Pleistocene levels—whose herpetofaunas have not yet been studied—may provide very interesting results in terms of environmental changes in the Cantabrian mountain zone.

## Acknowledgments

We thank Professors M. González Morales and L. G. Straus for having provided the materials that are the subject of this study. Professor G. Cuenca Bescós prepared the material, separating it from the micromammalian remains that she studied; she also provided critical help and information. Dr. Y. Fernández-Jalvo identified the rootlet markings on some of the bones. J. E. González efficiently facilitated our frequent consultations of the comparative collections in the Museo Nacional de Ciencias Naturales (CSIC). J. M. Rey provided critical information from his extensive modern owl pellet collections from northern Spain. The text was translated into English by Professor Straus, who also provided information on the site and feedback on earlier drafts. This study was partially supported by a Spanish Government grant, no. REN 2001-0466 and CGL 2008-03881.

## References Cited

- Bailon, S.  
1999 Diférentiation ostéologique des anoures (Amphibia, Anura) de France. *Fiches d'Ostéologie Animale, Archéologie* 1:41.
- Balcells, E.  
1975 Observaciones en el ciclo biológico de anfibios de alta montaña y su interés en la detección del inicio de la estación vegetativa. *Publicaciones Centro Pirenaico de Biología Experimental* 7(2):55-153.
- Barbadillo, L. J., J. I. Lacomba, V. Pérez-Mellado, V. Sancho, and L. F. López-Jurado  
1999 *Anfibios y reptiles de la Península Ibérica, Baleares y Canarias*. Planeta, Barcelona.
- Blain, H. A., S. Bailon, and G. Cuenca-Bescós  
2008 The Early-Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 261:177-192.
- Blain, H. A., S. Bailon, G. Cuenca-Bescós, J. L. Arsuaga, J. M. Bermúdez de Castro, and E. Carbonell  
2009 Long-term climate record inferred from Early-Middle Pleistocene amphibians and squamate reptile assemblages at the Gran Dolina cave, Atapuerca, Spain. *Journal of Human Evolution* 56:55-65.
- Böhme, G.  
1977 Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. *Wissenschaftliche Zeitschrift Humboldt-Universität Berlin (Math.-Nat. Reihe)* 36(3):283-300.
- Braña, F.  
1998 *Natrix natrix* (Linnaeus, 1758). In *Fauna Ibérica*, vol. 10, *Reptiles*, edited by A. Salvador, pp. 454-466. Museo Nacional de Ciencias Naturales, CSIC, Madrid.
- Clark Labs  
2000 Global Change Data Archive. Vol. 3. 1 km Global Elevation Model. CD-Rom, Clark University, Worcester, MA.
- Eastman, J. R.  
2001 Idrisi 32 release 2. Manual version 32.20. Clark Labs, Clark University, Worcester, MA.
- Esteban, M. L., and B. Sanchiz  
2000 Differential growth and longevity in low and high altitude *Rana iberica* (Anura, Ranidae). *Herpetological Journal* 10:19-26.
- Frost, D. R.  
2010. Amphibian species of the world: an online reference. Version 5.4 (8 April 2010). Electronic database accessible at <http://research.amnh.org/vz/herpetology/amphibia/>. American Museum of Natural History, New York.

- Gasc, J. P., A. Cabela, J. Crnobrnja-Isailovic, D. Dolmen, K. Grossenbacher, P. Haffner, J. Lescure, H. Martens, J. P. Martínez Rica, H. Maurin, M. E. Oliveira, T. S. Sofianidou, M. Veith, and A. Zuiderwijk  
1997 *Atlas of Amphibians and Reptiles in Europe*. Societas Europaea Herpetologica and Muséum National d'Histoire Naturelle, Paris.
- González Morales, M. R., and L. G. Straus  
2000a La Cueva del Mirón (Ramales de la Victoria, Cantabria): excavaciones 1996–1999. *Trabajos de Prehistoria* 57(1):121–133.  
2000b El depósito arqueológico de la Prehistoria reciente de La Cueva del Mirón (Ramales, Cantabria): bases estratigráficas para una secuencia regional. In *Actas do 3º Congresso de Arqueologia Peninsular*, edited by V. Oliveira Jorge, pp. 49–62. Vol. 4. ADECAP, Porto, Portugal.
- Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin  
2002 Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83:2027–2036.
- Holman, J. A.  
1998 *Pleistocene Amphibians and Reptiles in Britain and Europe*. Oxford University Press, Oxford, UK.
- ITGE  
1988 *Atlas geocientífico y del medio natural de la comunidad de Madrid*. Medio Ambiente. Instituto Tecnológico GeoMinero de España, Madrid.
- Lizana, M.  
2002 *Bufo bufo*. In *Atlas y libro rojo de los anfibios y reptiles de España*, edited by J. Pleguezuelos, R. Márquez, and M. Lizana, pp. 103–106. Dirección General de Conservación de la Naturaleza and Asociación Herpetológica Española, Madrid.
- Martín, C., and B. Sanchiz  
2010 Lisanfos KMS. Version 1.2. Online reference accessible at <http://www.lisanfos.mncn.csic.es/>. Museo Nacional de Ciencias Naturales, CSIC. Madrid, Spain.
- Pérez-Mellado, V., and G. Cortázar  
2002 Bases metodológicas del atlas de los anfibios y reptiles de España. In *Atlas y libro rojo de los anfibios y reptiles de España*, edited by J. Pleguezuelos, R. Márquez, and M. Lizana, pp. 21–32. Dirección General de Conservación de la Naturaleza and Asociación Herpetológica Española, Madrid.
- Pinto Llona, A. C., and P. J. Andrews  
1999 Amphibian taphonomy and its application to the fossil record of Dolina (middle Pleistocene, Atapuerca, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 149:411–429.
- Pleguezuelos, J. M., and S. Honrubia  
2002 *Elaphe scalaris* (Schinz, 1822). Culebra de escalera. In *Atlas y libro rojo de los anfibios y reptiles de España*, edited by J. Pleguezuelos, R. Márquez, and M. Lizana, pp. 201–283. Dirección General de Conservación de la Naturaleza and Asociación Herpetológica Española, Madrid.
- Pleguezuelos, J. M., R. Márquez, and M. Lizana (eds.)  
2002 *Atlas y libro rojo de los anfibios y reptiles de España*. Dirección General de Conservación de la Naturaleza and Asociación Herpetológica Española, Madrid.
- Salvador, A.  
1998 *Reptiles*. Vol. 10 of *Fauna Ibérica*, edited by M. A. Ramos et al. Museo Nacional de Ciencias Naturales (CSIC), Madrid.
- Salvador, A., and M. García-París  
2001 *Anfibios españoles. Identificación, historia natural y distribución*. Canseco Editores, Talavera de la Reina, Spain.
- Salvador, A., and J. M. Pleguezuelos  
2002 *Reptiles españoles. Identificación, historia natural y distribución*. Canseco Editores, Talavera de la Reina, Spain.
- Sanchiz, B.  
1980 Anfibios fósiles de la Cueva de la Paloma (Pleistoceno terminal, Asturias). In *La Cueva de la Paloma (Soto de las Regueras, Asturias)*, edited by M. Hoyos, pp. 101–108. Excavaciones Arqueológicas en España. Ministerio de Cultura, Madrid.
- Sanchiz, B., and J. M. Lobo  
2006 Restos herpetológicos de niveles auriniacienses de la Cueva de El Castillo (Puente Viesgo, Cantabria). In *En el centenario de la Cueva de El Castillo: El ocaso de los Neandertales*, edited by V. Cabrera, F. Bernaldo de Quirós, and J. M. Maíllo, pp. 403–416. Centro Asociado a la Universidad Nacional de Educación a Distancia en Cantabria, Santander, Spain.
- StatSoft Inc.  
2003 STATISTICA, data analysis software system and user's manual. Version 6.1. StatSoft Inc., Tulsa, OK.
- Straus, L., M. González Morales, W. Farrand, and W. Hubbard  
2001 Sedimentological and stratigraphic observations in El Mirón, a Late Quaternary cave site in the Cantabrian Cordillera, northern Spain. *Geoarchaeology* 16:603–630.
- Szyndlar, Z.  
1984 Fossil snakes from Poland. *Acta Zoologica Cracoviensia* 28(1):1–156.

**Table 14.1.** Number of fragments (FF) and minimum number of individuals (MNI) for each taxon and Holocene level in El Mirón Cave

Culture <sup>a</sup>	Level	<i>Salamandra salamandra</i>		<i>Alytes obstetricans</i>		<i>Bufo bufo</i>		<i>Rana temporaria</i>		<i>Anura indeterminate</i>	<i>Anguis fragilis</i>		<i>Natrix natrix</i>		<i>Natrix sp.</i>		<i>Coronella sp.</i>		<i>Elaphe sp.</i>		<i>Vipera sp.</i>	
		FF	MNI	FF	MNI	FF	MNI	FF	MNI	FF	FF	MNI	FF	MNI	FF	MNI	FF	MNI	FF	MNI	FF	MNI
BRN	03			1	1	8	1	9	3	5	5	1			1	1						
BRN	03.2							2	1		1	1										
BRN	03.4							1	1													
BRN/Fe	03.5					2	1	4	4				1	1			1	1				
BRN	03?							1	1													
CALC	04					2	1	3	1										1	1		
CALC	04-up					1	1	1	1													
CALC	05							6	2		1	1										
CALC	05.1?							1	1	1	7	1										
CALC	06					1	1	24	3		3	1										
CALC	07					1	1	7	2	2	6	1										
NEOL	08	1	1	2	1	10	3	65	7	8	8	1	1	1	2	1						
NEOL	09							42	7	4	1	1										
NEOL	09.6					1	1	45	6	2	2	1								1	1	
NEOL	09.7							4	3		1	1										
NEOL	09.8					1	1	8	3	1												
NEOL	10			1	1			27	3	1	4	1										
MESO	10.1									1					1	1	1	1				
<b>FF</b>	<b>356</b>	<b>1</b>		<b>4</b>		<b>27</b>		<b>250</b>		<b>25</b>	<b>39</b>		<b>2</b>		<b>4</b>		<b>2</b>		<b>1</b>		<b>1</b>	
<b>MNI</b>	<b>84</b>		<b>1</b>		<b>3</b>		<b>11</b>		<b>49</b>			<b>11</b>		<b>2</b>		<b>3</b>		<b>2</b>		<b>1</b>		<b>1</b>

<sup>a</sup>BRN: Bronze Age; Fe: Iron Age; CALC: Calcolithic; NEOL: Neolithic; MESO: Mesolithic

**Table 14.2.** Environmental values for areas having high ( $p > 50$ ) or low ( $p < 50$ ) probabilities of joint presence of *Bufo bufo* and *Rana temporaria* (group B+R) or *Anguis fragilis*, *Bufo bufo*, and *Rana temporaria* (group A+B+R), according to the habitat suitability models for each group

Group	Variables	N <sup>a</sup>	Mean	Minimum	Maximum	SD <sup>b</sup>	T p <sup>c</sup>
B+R	<b>Probabilistic suitability (<math>p &gt; 50</math>)</b>						
	precipitation (mm)	640	1,164.42	419.44	2,090.30	349.67	
	temperature (°C)	640	10.68	5.00	14.50	1.86	
	altitude (m)	640	757.65	5.00	1,994.00	416.39	
	insolation (sunlight hours)	640	2,001.13	1,583.92	2,313.58	98.16	
B+R	<b>Probabilistic suitability (<math>p &lt; 50</math>)</b>						
	precipitation (mm)	355	1,071.20	399.88	2,336.73	400.72	≤0.001
	temperature (°C)	355	11.54	5.80	14.80	1.49	≤0.001
	altitude (m)	355	590.23	4.00	1,730.00	344.23	≤0.001
	insolation (sunlight hours)	355	1,998.08	1,606.25	2,381.17	82.61	>0.05
A+B+R	<b>Probabilistic suitability (<math>p &gt; 50</math>)</b>						
	precipitation (mm)	532	1,274.50	604.85	2,090.26	311.82	
	temperature (°C)	532	10.88	5.00	14.80	2.02	
	altitude (m)	532	699.17	4.00	1,994.00	443.82	
	insolation (sunlight hours)	532	1,991.00	1,583.92	2,381.17	103.11	
A+B+R	<b>Probabilistic suitability (<math>p &lt; 50</math>)</b>						
	precipitation (mm)	463	972.83	399.88	2,336.73	368.00	≤0.001
	temperature (°C)	463	11.13	5.80	14.80	1.46	=0.03
	altitude (m)	463	692.17	6.00	1,916.00	344.60	>0.05
	insolation (sunlight hours)	463	2,010.44	1,606.25	2,307.25	78.34	≤0.001

<sup>a</sup>Number of meshes

<sup>b</sup>Standard deviation

<sup>c</sup>Probability of difference between the means of the two suitability areas (Student *T* test)

**Table 14.3.** Means and confidence intervals (95 percent) in the high habitat suitability models ( $p > 50$ ) for the joint presence of *Bufo bufo* and *Rana temporaria* (group B+R) or *Anguis fragilis*, *Bufo bufo*, and *Rana temporaria* (group A+B+R) for some relevant paleoclimatic variables

Group	Variables	Mean	Interval		Present <sup>a</sup>
B+R	Probabilistic suitability ( $p > 50$ )				
	precipitation (mm)	1,164	1,135	1,192	1,450
	temperature (°C)	10.7	10.5	10.8	13.0
A+B+R	Probabilistic suitability ( $p > 50$ )				
	precipitation (mm)	1,274	1,246	1,303	1,450
	temperature (°C)	10.9	10.7	11.1	13.0
	insolation (sunlight hours)	1,991	1,982	2,000	2,003

<sup>a</sup>Average values on the UTM 10 x 10 km square where El Mirón Cave is located