OBSERVED *vs.* POTENTIAL DISTRIBUTIONS: APPLICATION TO THE HERPETOFAUNA OF A REGION OF THE MEDITERRANEAN BASIN

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Abstract Observed (O) and potential (P) distributions are compared in order to distinguish between ecological and historical factors conditioning the ranges of amphibians and reptiles inhabiting the NE Iberian (Catalonia and Andorra). For this purpose, a tridimensional logistic model based on temperature, precipitation and altitude was used. Data were analyzed on the basis of the 10x10km UTM square. Sufficient data were available for 42 (of 47) species belonging to three major biogeographical groups ("European", Mediterranean and Pyrenean endemics) to perform the analysis. Three different kinds of results were obtained. O=P indicates that ecological variables provide a reliable explanation for the complete distribution. O>P means the same but with insufficient scale precision. Excluding the random effects, O<P (found nearly in the 50% of the species) implies the influence of historical factors: isolation, lack of range stability (expansion-regression) and range independence (competitive interactions). For each case some examples are given and discussed using the literature.

Περίληψη Συγκρίνονται οι παρατηρούμενες (Ο) και οι εν δυνάμει (P) κατανομές των αμφιβίων και των ερπετών της ΒΑ Ιβηρικής (Καταλωνίας και Ανδόρρας) με στόχο να διακριθούν οι οικολογικοί από τους ιστορικούς παράγοντες που τις ρυθμίζουν. Για το σκοπό αυτό χρησιμοποιήθηκε ένα τρισδιάστατο λογιστικό μοντέλο, βασισμένο στη θερμοκρασία, τα κατακρημνίσματα και το υψόμετρο. Υπήρχαν διαθέσιμα ικανοποιητικά στοιχεία για 42 (από 47) είδη που ανήκουν σε τρεις κύριες βιογεωγραφικές ομάδες ("Ευρωπαϊκά", Μεσογειακά και ενδημικά των Πυρηναίων). Προέκυψαν τρία διαφορετικά αποτελέσματα. Όταν Ο=P οι οικολογικές παράμετροι προσφέρουν αξιόπιστη ερμηνεία της συνολικής κατανομής. Όταν Ο>P ισχύουν τα ίδια, αλλά μεανεπαρκή ακρίβεια κλίμακας. Εξαιρώντας τις τυχαίες επιδράσεις, το Ο<P (κάτι που βρέθηκε στο 50% των ειδών) δηλώνει την επίδραση ιστορικών παραγόντων: απομόνωσης, ασταθούς κατανομής (επέκτασης-συρρίκνωσης) και ανεξαρτησίας της κατανομής (ανταγωνιστικών αλληλεπιδράσεων). Για κάθε περίπτωση δίνονται και συζητώνται παραδείγματα από τη βιβλιογραφία.

INTRODUCTION

The comparison between the observed distribution of species and their potential range deduced from ecological parameters can give information about the historical influences conditioning their biogeography (ANTÚNEZ & MENDOZA 1992). Amphibians and reptiles are good subjects for this kind of analysis since most of them are abundant and easily detected and their dispersion abilities are low. Catalonia and Andorra represent an interesting biogeographical region since the herpetofauna found is very diverse and numerous: 51 species (14 amphibians and 37 reptiles, see LLORENTE *et al.* 1995 and Table 1). This high species richness has been explained by the frontier effect (i.e. increase of range heterogeneity) between Mediterranean and non-Mediterranean areas of the Iberian

Table 1 Amphibian and reptilian species of Catalonia and Andorra belonging to the different biogeographical groups. ME = Mesoeuropean; WE = Western European; ES = Eurosiberian; PE = Pyrenean endemit; IB = Iberomediterranean; IM = Iberomagrebian; CM = Circummediterranean., RI = Recently introduced, OI = Old-introduced (both Mediterranean), M = Marine. O=P = observed distribution roughly equivalent to potential. O>P = observed distribution larger than potential due to microhabitat use. O<P = observed distribution smaller than potential due to isolation (1), random effects (2), regression (3), expansion (4), and/or competitive interactions (5). ID = insufficient data.

AMPHIBIA (14 species)		REPTILIA (37 species)			
URODELA		**CHELONIA**		**SAURIA**	
Salamandra salamandra	ES $O<P^1$	Testudo hermanni	CM $O<P^3$	Tarentola mauritanica	IM $O>P$
Euproctus asper	PE $O<P^1$	Emys orbicularis	ES $O<P^3$	Hemidactylus turcicus	OI $O=P$
Pleurodeles waltl	IM $O=P$	Mauremys leprosa	IM $O=P$	Psammodromus algirus	IM $O>P$
Triturus helveticus	WE $O<P^1$	Trachemys scripta	RI ID	Psammodromus hispanicus	IB $O<P^2$
Triturus marmoratus	WE $O<P^1$	Caretta caretta	M -	Acanthodactylus erythrurus	IM $O<P^{1,3}$
ANURA		Chelonia mydas	M -	Lacerta lepida	IB $O>P$
Discoglossus pictus	OI $O<P^4$	Dermochelys coriacea	M -	Lacerta viridis	ME $O<P^{1,5}$
Alytes obstetricans	WE $O=P$	**OPHIDIA**		Lacerta agilis	ES $O=P$
Pelobates cultripes	IB $O=P$	Coluber hippocrepis	IM $O=P$	Lacerta vivipara	ES $O=P$
Pelodytes punctatus	WE $O>P$	Coluber viridiflavus	WE $O<P^{1,5}$	Lacerta bonnali	PE ID
Bufo bufo	ES $O=P$	Malpolon monspessulanus	CM $O>P$	Lacerta aranica	PE ID
Bufo calamita	WE $O>P$	Elaphe scalaris	IB $O>P$	Lacerta aurelioi	PE ID
Hyla meridionalis	IM $O=P$	Elaphe longissima	ME $O<P^{1,5}$	Podarcis muralis	ME $O<P^{1,5}$
Rana perezi	IB $O>P$	Natrix maura	WE $O>P$	Podarcis hispanica	IM $O>P$
Rana temporaria	ES $O<P^{1,5}$	Natrix natrix	ES $O=P$	Podarcis pityusensis	RI ID
AMPHISBAENIA		Coronella austriaca	ES $O<P^{1,5}$	Anguis fragilis	ES $O=P$
Blanus cinereus	IM ID	Coronella girondica	IM $O>P$	Chalcides striatus	IB $O=P$
		Vipera aspis	WE $O<P^5$	Chalcides bedriagai	IB $O=P$
		Vipera latasti	IM $O<P^{3,5}$		

Peninsula in this region (RIBA *et al*. 1976) as well as the confluence of elements belonging to different biogeographical origins: "European" (including Western European, Mesoeuropan and Eurosiberian species), Mediterranean (Ibero-mediterranean, Ibero-magrebian and Circum-mediterranean) and Pyrenean endemics (see Table 1). This study attempts to distinguish between abiotic environment and other factors (biotic, geographical, historical) comparing observed and potential distributions of amphibians and reptiles in the NE region of Iberian Peninsula.

MATERIAL AND METHODS

The study area covers 38,800 km^2 in the NE Iberian Peninsula (Fig.1). The most relevant geographical units (see RIBA *et al*. 1976) are: the Pyrenees and Prepyrenees (N), the Montseny massif (center-E), the Prelittoral Chain, the Besseit mountains (S), the central depression (center-W) and the Empordà plain (NE). The basic description of temperature, precipitation and altitude is shown in Fig.1. For methodological purposes all data were mapped on a UTM projection grid and the unit of analysis was a 10x10 km square (Fig.1, 2). Each square was prospected in search of all the amphibian and reptile species. Although observations were assumed to be reasonably accurate for estimating the actual distribution of most species, the heterogeneous sources of information together with the high variation in the populational features among species prevented the consideration of abundances. Thus, only presence/absence data were considered in each unit (see more details in LLORENTE *et al*. 1995).

Furthermore, all the squares were also typified for three variables: mean temperature of the hottest month (August), total annual rainfall and mean altitude (Fig.1). Although other variables (vegetation, soil, lithology etc.) could have also been used, only the former were considered to be ecologically reliable due to the scale of data used in this study (ANTÚNEZ & MENDOZA 1992). Environmental data were obtained from RIBA *et al*. (1976). For each species, the values of the habitat variables in the squares where this was observed were considered. In order to determine the probability of presence of each species in each square, a logistic function (WALKER 1990, MANN *et al*. 1991) was used:

$$p = e^y / (1 + e^y)$$

where p is the probability of presence and y is a equation of regression as:

$$y = a + bx_1 + cx_2 + ... + nx_n$$

where xi are the variables incorporated to the model increasing its statistical significance. The forward method was preferred instead of the stepwise in order to always produce a tridimensional model using all three variables and to facilitate the comparison between species. The parameters of the equation were estimated by maximum likelihood and tested by Wald tests. Models for each species were assessed by χ^2 test of goodness of fit..

Subsequent potential distributions at the 95% level were obtained through this model for each species and compared with distributions observed (Fig.2) (see GULVE 1994
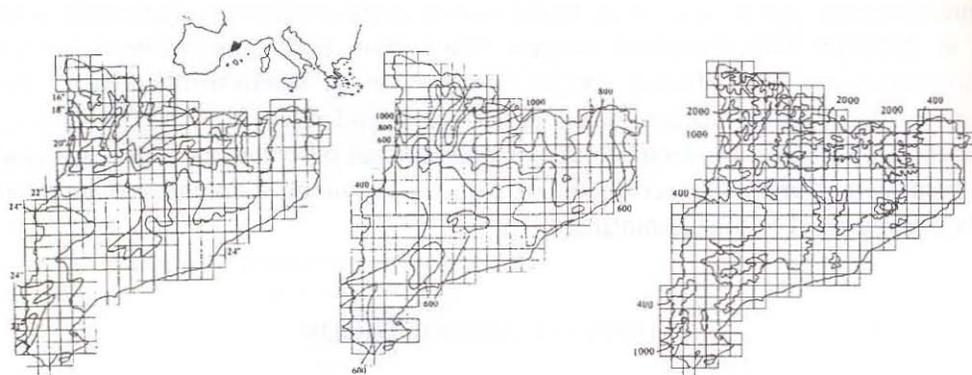
Fig.1 Distribution of mean temperature of August, annual precipitation and altitude (from left to right) in the study area.

and ROMERO & REAL 1996 for more comments). These results were then evaluated in the light of the published information on those species inside and outside the study area, allowing the interpretation of the factors influencing their distribution.

RESULTS AND DISCUSSION

Table 1 summarizes the results of comparing observed and potential distribution in the different species. Of the 51 species available, 9 were excluded because of lack of information (6 spp.) or because they are marine (3 spp.). Some indicative examples of different kinds of relationship between distributions are illustrated in Fig.2.

The anuran *Pelobates cultripes* is an example of species showing coincidence between observed and potential distribution. In this case, ecological variables provide a reliable explanation for the complete distribution of this species in the study area, and other factors are negligible. Similar patterns were obtained for 14 species, 5 amphibians (including the example) and 9 reptiles (Table 1). These were either strongly Mediterranean or euryoecous species (LLORENTE *et al.* 1995).

The observed distribution of the Mediterranean lizard *Psammodromus algirus* exceeds the potential distribution in the southern slopes of the Pyrenees (Fig.2). In contrast with the former case, the model does not explain this pattern. It might be interpreted not as a deficiency in the environmental variables chosen but a question of insufficient scale precision. Penetration of this species northwards along the valleys (which provide a suitable microhabitat not detected by the 10x10km² UTM grid) has been described elsewhere (BAUWENS *et al.* 1986). Thus, ecological requirements are once more enough to explain these patterns. Eleven-twelve species (3 amphibians and 8-9 reptiles), all belonging to the Mediterranean group, showed a similar pattern (Table 1). The case of *Psammodromus hispanicus* is similar but, despite the reasonably good sampling, it has not been found in some favourable localities within its potential range. This opportunist species suffers high demographic fluctuations and often becomes locally extinct
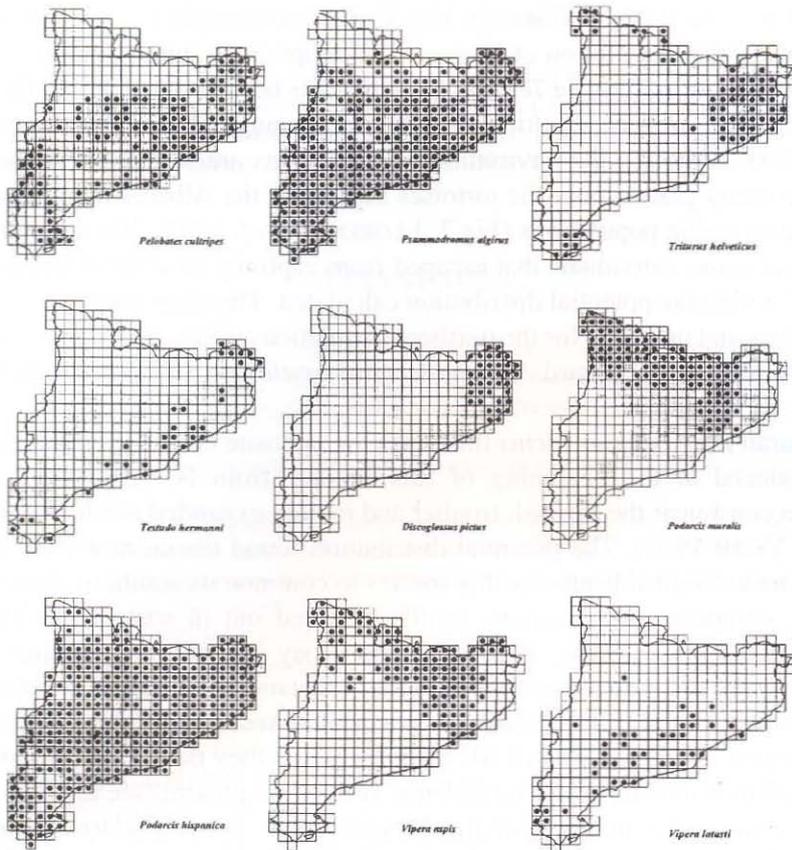
Fig.2 Some examples of different kinds of actual-potential distribution relationships of amphibians and reptiles from Catalonia and Andorra (for explanations, see text and table 1). Dots = actual distribution. Shaded areas = potential distribution.

(CARRETERO 1993). It provides a good example of random affecting distribution. The aspect should not be forgotten in the rest of the cases.

Conversely, in other species, the observed range has been found to be substantially smaller than the potential. In those cases, it is inferred that the geographical pattern in the study area is due not only to abiotic environmental constraints but also to other factors. The additional information found in the literature gives some explanations.

The newt *Triturus helveticus* (as well as its congeneric *T. marmoratus*, not represented here) shows an apparent discrete pattern (Fig. 2). In fact, all the northern localities are connected through the northern slopes of the Pyrenees (ARNTZEN 1989). Moreover, these are in their turn connected with the southern range through several populations in the Aragón region (east of Catalonia) following the Ebro river in NW-SE direction (FALCON & CLAVEL 1987). Thus, isolation between river basins is more responsible for the distribution found than any environmental feature (REAL 1991). Another similar effect has been detected in some "European" and Pyrenean species whose southern populations have become locally extinct in isolated mountains (Table 1). Isolation (including geographic

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disjunction of peripheral populations, see GULVE 1994) is thought to be mainly or partially determinant for the distribution of 10 species (5 amphibians and 5 reptiles) .

The Mediterranean tortoise *Testudo hermanni* has been affected during the last three centuries by human impact resulting in a strong demographic and range regression (CHEYLAN 1984). Although the environmental conditions are apparently favourable for this species in many places, only the tortoises inhabiting the Alberes mountains close to France belong to viable populations (Fig.2, LLORENTE *et al.* 1995). The remains of other populations and some individuals that escaped from captivity have been found along the Catalan coast, within the potential distribution calculated. The same applies to the terrapin *Emys orbicularis* and probably for the northern populations of the viper *Vipera latasti* (see below) and the thermophile lizard *Acanthodactylus erythrurus* (CARRETERO & LLORENTE 1995).

The anuran *Discoglossus pictus* illustrates the opposite case. This species was accidentally introduced at the beginning of this century from N. Africa to the French Mediterranean coast near the Spanish frontier and rapidly expanded north- and southward (MARTENS & VEITH 1987). The potential distribution found demonstrates (as predicted) that there are no ecological limits for this species to continue its southern expansion.

Finally, competitive interactions cannot be ruled out in some cases (MARCO & POLLO 1993, ROMERO & REAL 1996). Isolation may explain the absence of some "European" species from unconnected southern mountains within their potential ranges (see above). However, only the presence of their Mediterranean equivalents explains why they do not appear in other places of NE Spain, whereas they do appear in many similar areas of the Italian Peninsula where no endemic species are present (see ENGELMANN *et al.* 1986). This seems to be the case of the Mesoeuropean lizard *Podarcis muralis* with regards to the Mediterranean *P. hispanica* (see Fig.2). Both species may overlap in few localities both strong spatial segregation between them has been reported in such places (ARNOLD 1987, BARBADILLO, 1987). Other species tandems showing feasible interactions are *Coluber viridiflavus - Malpolon monspessulanus, Elaphe longissima - E. scalaris* and *Lacerta viridis - L. lepida*. The interesting case of *Vipera aspis - V. latasti* merits further comment since the interaction is modified by human disturbance. Habitat fragmentation affecting mainly Mediterranean areas as well as a vulnerable trophic strategy have produced regression of *V. latasti* whereas *V. aspis* is little disturbed and its southeastern range is even increasing (see more extensive comments in PARELLADA 1995). Both species are absent in NE Catalonia (Fig.2).

To sum up, although the abiotic environment is important to explain distribution patterns, after excluding scale and random factors, nearly 50% of the Catalan and Andorran herpetofauna shows some evidence of other factors conditioning its range. These limitations consist mainly of isolation and the lack of range stability and range independence. Thus, potential distribution should always be taken into account when analyzing distributions and when applying the results to species management and conservation decisions (i.e. remedial action for declining population, reintroductions, design of protected areas, etc., RAMÍREZ & VARGAS 1992).

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