ALTITUDINAL DISTRIBUTION
OF AMPHIBIANS AND REPTILES
IN THE SPANISH PYRENEES [1]

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SUMMARY.— This paper analyzes the distribution in altitude of about 3.400 data belonging to the 37 most common species of Pyrenean amphibians an reptiles, with localities ranging from sea level to 3.000 m. For every species the mean, standard deviation and range have been calculated, with the purpose of ordering the species on their mean altitude; several groups can be so distinguished. Both abundance of observations and species richness decrease with altitude, but that inverse relation seems to depend not only on the climatic factors linked to altitude, but also on the low observation opportunities existing at the top mountain levels. Diversity of Pyrenean herpetocoenoses is fairly hihg, reaching 91,6 % of the theoretical meximum at low altitudes. Similarity between altitude distribution of different species allows a clustering of the data, with a separation of six especies groups, not quite similar to those obtained from the mean altitude only. These groups include species from high mountain areas, middle-hihg forested areas, lowland species, ubiquist species and so on.

RESUMEN.— Este trabajo analiza la distribución en altitud de unos 3.500 datos correspondientes a las 37 especies más comunes de anfibios y reptiles pirenaicos, cuyas localidades de captura se escalonan entre 0 y 3.000 m. Para cada especie se ha calculado la altitud media de las citas, así como la correspondiente desviación típica y el rango de variación. Se distinguen así varios grupos de especies, aunque ampliamente solapados. Tanto la abundancia de las observaciones como la riqueza específica disminuyen con la altitud, pero esta relación inversa parece no ser solamente consecuencia de los factores climáticos ligados a la altitud, sino también de las menores oportunidades de observación propias de la alta montaña. La diversidad en las herpetocenosis pirenaicas es bastante alta, alcanzando en algunos niveles el 91,6 % del máximo teórico. La mayor o menor similaridad entre las distribuciones en altitud de las distintas especies permite agrupar las mismas en seis conjuntos, que no coinciden por completo con los derivados exclusivamente de la altitud media. Estos grupos incluyen especies de alta montaña, de bosque montano medio, de zonas bajas, especies ubicuas, etc.

RESUME.— Dans ce travail on analyse la répartition en altitude de quelque 3.500 données, correspondant a les localités de capture ou observation des 37 especes les plus communes d'amphibiens et de reptiles pyrénéens, dont les altitudes de capture s'étalent entre le niveau de la mer et 3.000 m. Pour chaque espece on a calculé l'altitude moyenne des localités, leur déviation standard et les valeurs minimum et maximum. On peut séparer donc quelques groupes d'especes, bien qu'ils son largement imbriqués. La frequence des observations et la richesse specifique descendent avec l'altitude; cette rélation inverse n'est pas seulement consequence des facteurs climatiques, mais aussi des oportunités d'observation, qui sont moindres dans la haute montagne. La diversité des herpétocenoses pyrénéennes est plutôt haute, et elle arrive, dans certaines altitudes, au 91,6 % du maximum théorique. La ressemblance entre les répartitions en altitude des differents especes peut etre évaluée, et sert à faire des groupements, plus marqués que ceux dérivés exclusivament de l'altitude moyenne. Ces groupes sont six, avec des especes de haute montagne, de forêt montane, thérmophiles, ubiquistes, etc.

Key words: *Amphibians, Reptiles, Distribution, Altitude, Diversity, Pyrenees.*

Works dealing with geographic distribution of Spanish amphibians and reptiles have had a clear progress in the last years, not only in the Pyrenean region (BERGERANDI, 1981; MARTÍNEZ RICA, 1983; VIVES, 1983; BEA et al., 1985; FALCON & CLAVEL, 1987, etc.), but also in the whole of Spain (BAS, 1981; BARBADILLO, 1983; PÉREZ MELLADO, 1983, etc.). The number of available data is now enough to allow some elementary analysis which show several features of the distribution of Pyrenean amphibians and reptiles.

The word "distribution" is frequently understood as "spatial" or "geographic" distribution. This is, however, only an aspect of animal distribution, the one linked with spatial dimensions of an ecological niche. Other dimensions, such as time, food, homospecific or heterospecific interactions, and so on, represent, as everyone knows, independent axes which serve also to study the distribution of animals upon them.

In this paper we analyze only one of the distributional dimensions, that is, altitude. Of course, this factor heavily affects animal distribution, mainly in the heterothermic animals (amphibians and reptiles, for instance), which depend strictly on environmental factors, such as temperature and rainfall, closely linked to elevation.

The starting point of our paper is a set of altitude data corresponding to capture localities of Pyrenean amphibians and reptiles. We do not consider other factors than altitude, although other geographic, climatic and historic factors may have even more weight than elevation in the distribution of a species along an altitudinal gradient.

To consider only one variable, ignoring spatial coordinates, may seem sensible, but this paper would be too long if not limited in this way. Besides that, spatial distribution of Pyrenean herptiles is the subject of another paper, now underway. Altitude, of course, cannot be treated as a third spatial dimension, as it is strongly linked to so many evironmental factos and has several exclusive features. There is a third reason for reducing the scope of this paper: although altitude effects on animal distribution varies from place to place, and so the reader may object the general conclusions derived from a so complex region, the authors believe in the "large numbers law": when the number of observations is large enough, the errors coming from an uneven sampling plan or from the heterogeneity of studied area tend towards a mutual cancellation, so revealing the non-random structures of the distribution. Of course, these features do not show themselves so clearly as they do in other instances whitout random or systematic "noise", but the analysis allows, however, some valid inferences and hence is worth realising.

1. Material and methods

a) *Study area:*

The studied area is shown in fig 1. The superimposed grid is the standard UTM grid, with squares of 100 x 100 Km.; the outer limits follow the borders of smaller squares, and are rather conventional. In a region as complex as the Pyrenees, delimitations made on some geographical or ecological feature are very difficult and, in fact, also conventional. The delimitation we have chosen offers some practical advantages, as it is also used on other works of zoological or botanical cartography in the Pyrenees.

The area of studied region is 46800 Km². Such a large extension, together with the environmental complexity of the zone, and with a long biogeographic history in which Pyrenees were both a barrier and a communication path, give to the Pyrenean herpetofauna the features of a varied mosaic made of elements of diverse origin and history. Altitude is a main factor which patterns such a mosaic in a set of natural communities more or less adapted to mountain conditions.

We have hesitated about the inclusion of data from the French Pyrenees in ou work; it is clear that the Pyrenean range is an unitary whole, without artificial administrative barriers. Moreover, while not so
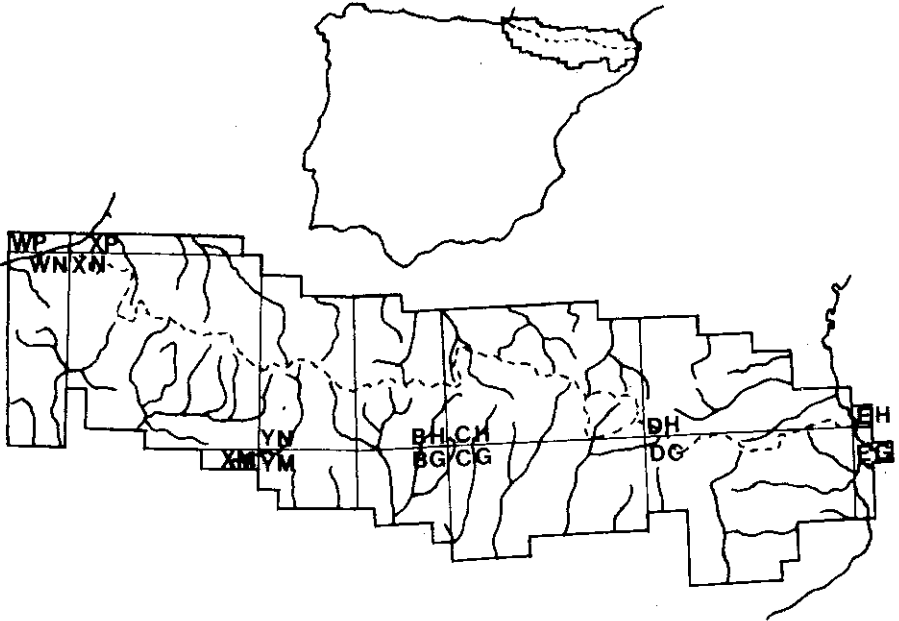
Fig. 1.—Sketch of studied area. Superimposed is shown the UTM grid of 100 x 100 Km. *(Esquema del área estudiada. Se ha superpuesto la cuadrícula UTM de 100 Km. de lado).*

numerous as the Spanish ones, French data are quite numerous, and their absence would be sensible. Lastly, for the mountain species at least, the divide line is not a barrier, because the same populations are found on both sides of it. Nevertheless, the inclusion of French data modifies the results, which could be clearer if belonging only to one slope. As we have said, the influence of altitude is masked by the heterogeneity coming from the inclusion of both Pyrenean sides.

We have chosen an intermediate approach: to work with data from the north and south sides, but, as conclusions are not so clear for the whole Pyrenean area, they apply only to the Spanish slopes; hence the title of the paper.

b) *Construction of the hypsometric curve:*

The studied area has been divided into 17 altitude classes, from sea level to the highest peak of the range (Mt. Aneto, 3404 m); each class is, then, 200 m. wide. The surface of the classes has been estimated

TABLE 1

Altitude intervals and number of observations for amphibians and reptiles

Altitude (m.)	Area (Km²)	Cumulative % área	Observations amphibians	Observations reptiles
0-200	4084.9	8.9	130	197
200-400	3256.2	16.0	52	93
400-600	6253.9	29.6	151	288
600-800	7153.2	45.2	188	345
800-1000	6318.5	59.0	323	354
1000-1200	4436.7	68.6	185	250
1200-1400	3314.2	75.9	133	159
1400-1600	2707.2	81.8	125	86
1600-1800	2238.2	86.6	85	50
1800-2000	1830.4	90.6	91	52
2000-2200	1541.3	94.0	72	34
2200-2400	1297.7	96.8	42	22
2400-2600	932.6	98.8	5	3
2600-2800	420.4	99.8	1	1
2800-3000	85.9	99.95	—	3
3000-3200	22.2	100	—	—
3200-3404	0.6	100	—	—

using an old method (attributed to DARWIN) which, although appearing inaccurate, allows a better precision than the use of planimeters and is almost as good as a digitizer pad: we have cut from an adequate map the different altitude classes, following their borders, and have weighted the paper with a sample-scale, obtaining the surface estimates through a simple proportion. The results are given in table 1.

c) *List of species:*

We have considered only the species of amphibians and reptiles inhabiting the Pyrenees not exceedingly scarce. All species observed at least ten times before 1985 were included - that means 14 amphibian and 23 reptilian species, about 60 % of Spanish and 84 % of the Pyrenean herpetofaunas. The list of species, with the number of observations for all of them, is shown in tables 2 and 3.

TABLE 2

Distribution in altitude of pyrenean amphibians

SPECIES	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20	20-22	22-24	24-26	26-28	(m x 100)
Euproctus asper	2	4	11	17	28	27	15	26	16	22	16	12	1	1	
Sal. salamandra	6	11	12	18	23	25	25	21	11	4	3	2	1	0	
Triturus helveticus.......	9	4	22	12	12	12	4	8	11	12	7	2	0	0	
Triturus marmoratus.....	15	1	11	10	2	8	4	0	0	0	0	0	0	0	
Discoglossus sp.	10	1	3	4	8	0	0	0	0	0	0	0	0	0	
Alytes obstetricans	10	4	13	30	63	33	32	15	10	9	8	4	0	0	
Pelobates cultripes	7	1	0	1	0	0	0	1	0	0	0	0	0	0	
Pelodytes punctatus	7	2	2	7	13	2	0	0	0	0	0	0	0	0	
Hyla arborea	1	1	10	2	9	3	1	0	0	1	0	0	0	0	
Hyla meridionalis	11	3	0	1	1	0	2	0	0	0	0	0	0	0	
Bufo bufo	23	10	19	34	63	30	23	11	5	5	3	1	0	0	
Bufo calamita	7	1	9	12	35	4	3	2	0	0	2	0	0	0	
Rana perezi	20	9	32	30	47	13	4	0	0	0	0	0	0	0	
Rana temporaria	2	0	8	10	19	27	20	41	32	28	33	21	3	0	

TABLE 3

Distribution in altitude de pyrenean reptiles

SPECIES	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20	20-22	22-24	24-26	26-28	28-30 (m x 100)
Mauremys leprosa	11	2	0	1	0	0	0	0	0	0	0	0	0	0	0
Tarent. mauritanica......	17	2	6	5	3	0	0	0	0	0	0	0	0	0	0
Anguis fragilis	16	5	21	31	30	28	9	11	6	6	1	0	0	0	0
Lacerta lepida	14	2	15	28	32	12	2	0	0	1	1	0	0	0	0
Lacerta agilis	0	1	0	2	0	0	3	2	2	0	2	1	0	0	0
Lacerta viridis.........	9	5	15	14	16	19	12	2	2	3	0	2	0	0	0
Lacerta vivipara........	1	0	3	10	4	6	3	8	4	3	4	7	2	1	1
Lacerta monticola	0	0	0	0	0	0	0	0	0	1	4	7	2	1	0
Podarcis hispanica	16	9	15	27	32	19	10	3	1	1	0	0	0	0	0
Podarcis muralis........	17	14	14	27	37	31	50	26	16	11	8	6	0	0	0
Psammod. algirus.......	12	2	7	11	6	2	1	0	0	0	0	0	0	0	0
Chalcides chalcides	6	1	10	7	5	3	0	0	0	1	0	0	0	0	0
Colub. viridiflavus......	1	3	8	8	7	11	18	4	3	1	0	0	0	0	0
Coronella austriaca	4	1	2	7	6	13	6	7	3	8	3	0	0	0	0
Coronella girondica	3	5	13	20	29	13	6	1	1	1	0	0	0	0	0
Elaphe longissima	8	4	6	10	6	3	1	0	0	0	0	0	0	0	0
Elaphe scalaris	7	6	31	27	15	7	3	0	0	0	0	0	0	0	0
Mal. monspessulanus ..	10	6	38	33	39	10	5	0	0	0	0	0	0	0	0
Natrix maura	18	9	44	35	30	22	6	0	0	0	0	0	0	0	0
Natrix natrix	16	6	17	18	19	10	8	2	0	0	0	0	0	0	0
Vipera aspis	4	4	17	16	33	35	14	19	10	16	11	6	1	0	2
Vipera latastei	0	0	2	4	6	2	1	0	2	0	0	0	0	0	2
Vipera seoanei	7	6	4	4	3	0	0	0	0	0	0	0	0	0	0

d) *Origin of data:*

All data were taken from the computer file formed and mantained in the Pyrenean Institute of Ecology by one of the authors (J.P.M.R.). This file had, when our paper started, about 7400 data on Spanish amphibians and reptiles (now it has over 17000), and gave about 2000 Pyrenean localities; we contributed 1500 more data, still not on file and taken from collections or from the literature.

The total number of available data was 3520 observations, 1583 for amphibians and 1937 for reptiles. The number is large enough to allow for some unevenness in the data and to reveal some general features of the distribution of Pyerenean herpetofauna in altitude, in spite of area heterogeneity.

e) *Methods of analysis:*

We have used clasical statistical or clustering methods, mainly non-parametric procedures, because the data do not support parametric ones. These procedures are given in the text where needed, but no description is attempted because all methods are widely known.

2. Results: The altitude distribution of species

The basis for all analysis was the rough distribution of observations in every altitude class. Such a distribution is shown in tables 2 for amphibians, and 3 for reptiles. Looking at the tables we can see several important points.

First, the amplitude of distribution ranges stands out: many species have a broad altitude range, probably because the country is so diverse. As we have said, inclusion of data from northern slope increases the variety of localizations in Atlantic and middle-European species, which are found at low altitude on the northern side of the chain and at high altitude in the south. Moreover, the climatic constraints of the western (Atlantic) and eastern (Mediterranean) ends of the chain limit the distribution of some species, which are found only there, and hence at low altitude, while in the whole of their area they may be found in high places. The most striking instance of such a wide range is *Vipera aspis*, a species found from sea level, on the Catalonia coast to about 2900 m. in the central Pyrenees.

Notwithstanding the broad ranges and the large overlap between them, it is clearly feasible to order the species along an altitudinal gradient, from the lowland to high mountain, taking only their mean altitude. Although the structure of such an ordination changes from place to place, we may get an order rather general, a kind of frame for the whole chain, if not a compulsory pattern for every species. We present this ordination in figure 2.
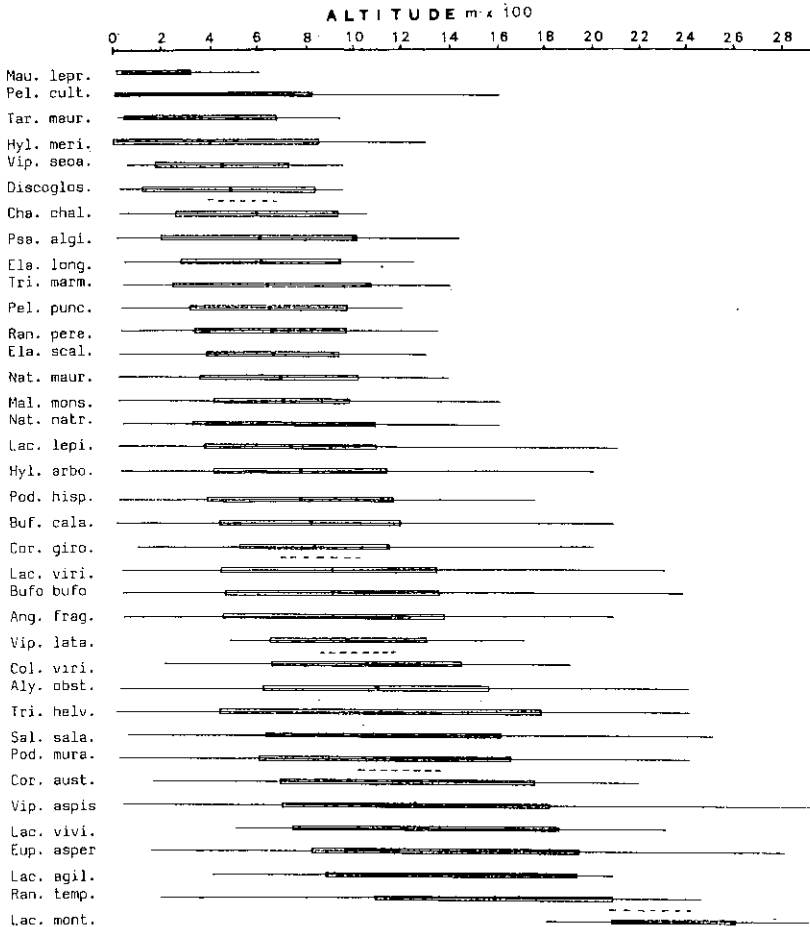

Fig. 2.—The Pyrenean species of amphibians and reptiles, ordered after the mean altitude of their localities. The altitude ranges and the standard deviations are also drawn. *(Ordenación de las especies pirenaicas de anfibios y reptiles, de acuerdo con la altitud media de sus localidades. Se ha representado el rango de distribución altitudinal de cada especie, y las correspondientes desviaciones típicas).*

It would be interesting to divide the species into groups according their mean altitude, but the ranges are so widely overlapped that we get only a crude and rather subjetive classification. See, however, a more sound attempt of classification in later pages. For the present, two groups of species stand clearly out in both extremes of the range. At the low end we see a group of mediterranean species *(Mauremys leprosa, Pelobates cultripes, Tarentola mauritanica, Hyla meridionalis* and *Discoglossus aff. pictus)* together with a cantabrian species, *Vipera seoanei,* which enters artificially into this group due to effects of area delimitation. For the species in this group mean altitude does not surpass 600 m.

At the opposite end we find, together with a Pyrenean endemic strictly linked to the highest levels *(Lacerta monticola bonnali),* six high mountain species whose mean altitude exceeds 1300 m. These species are *Coronella austriaca, Lacerta vivipara, Euproctus asper, Lacerta agilis, Rana temporaria* and *Vipera aspis.* The latter two species can be found, nevertheless, in lowland areas, respectively in the western and eastern ends of the chain.

Between both groups are the remaining 24 Pyrenean species, whose distribution is determined not so much by altitude as by other environmental factors; this group is a mixture without an adequate name (perhaps mediterranean-montane would be descriptive enough, as, within this group, mediterranean and montane species are at the opposite ends).

Standard deviations corresponding to each species are rather large. This is due not only to the broad altitudinal ranges, but also to asymmetry or irregularity of distributions. Both causes are, as we have said, a consequence of the complex features of the Pyrenean landscape. That prevents us from distinguish between the eurihipsic and stenohipsic species, but reveals a relation between mean altitude and dispersion of data: the species from high places have wider altitude dispersions than those from lowland areas. A positive correlation between mean values and their correspondng dispersions is trivial, and may be expected in almost any kind of sample. But in the present case the signification level of such a correlation is so high ($> 99.9 \%$) that we can confidently believe in real factors increasing the relation. Of course, one of the main factors among these is the mixing of French and Spanish data: on the northern slope there are several lowland species that, in the south, live only in the mountains, while the opposite, that is, southern mediterranean species living also in the mountains of the north side is neither true nor possible. So, as the main

bulk of data comes from southern slopes, lowland species have smaller standard deviations than mountain species.

Looking at the main taxonomic groups mean altitude is related to the water needs of each group. So, the average altitudes of urodela, anura, sauria and ophidia are, respectively, 1170, 1021, 920 and 860 m. This result agrees with that of MARTINEZ RICA (1979) for the Aragonese Pyrenees, but differs from those reported by PLEGUEZUELOS (1986) for the reptiles of southern Spanish mountains.

3. Results: Joint distribution

Everyone knows the strong influence altitude has in the distribution of animals. For amphibians and reptiles, such an influence is more important than for other groups which have better thermoregulation systems, or which, by their smaller size or greater mobility, can take best advantage of small refuges or adequate microclimates.

Altitude has an effect on animal distribution in several ways: First, through environmental factors, mainly temperature and rainfall, which are clearly dependent on it. Second, through biogeographic or historic factors linked to climatic changes in the past and to the "island structure" of high mountain ecosystems. Third, through different human actions, that is, by transport or artificial extinction of species. And fourth, through the action of other animals which compete with, feed on, or serve as food for the considered species.

To these factors we can add another, which is rather artificial: as we consider all available data, these being not taken by a sampling plan, results are dependent on different searching times, which are shorter for high mountain areas than for lowland ones. High mountain areas are, then, poorly represented on the whole, and that distorts the distribution.

To evaluate the different importance of some of the preceding factors we have analyzed data for every species and for all of them jointly. The total number of observations in each altitude class has been correlated to corresponding altitude, using the SPEARMAN ordinal procedure. The results are shown in table 4. Correlation coefficients are negative for all species, that is, the number of observations increase at low altitudes, as can be obviously expected. This relation is almost always very significant, with a probability of over 99 % in 16 species, and over 99.9 % in seven of them. *Podarcis hispanica* shows the highest correlation coefficient, perhaps due to its absence of almost all

TABLE 4

Correlation between altitude and number of observations for pyrenean amphibian and reptiles

Species name	Spearman R	Signification
Euproctus asper	—0.52	95 %
Salamandra salamandra	—0.76	99.9 %
Triturus helveticus	—0.72	99 %
Triturus marmoratus	—0.39	—
Alytes obstetricans	—0.71	99 %
Discoglossus cf. pictus	—0.45	90 %
Hyla arborea	—0.65	99 %
Hyla meridionalis	—0.55	99 %
Pelobates cultripes	—0.21	—
Pelodytes punctatus	—0.63	99 %
Bufo bufo	—0.85	99.9 %
Bufo calamita	—0.71	99 %
Rana perezi	—0.64	99 %
Rana temporaria	—0.21	—
Mauremys leprosa	—0.15	—
Anguis fragilis	—0.79	99.9 %
Tarentola mauritanica	—0.46	90 %
Lacerta agilis	—0.10	—
Lacerta lepida	—0.71	99 %
Lacerta monticola	—0.56	95 %
Lacerta viridis	—0.84	99.9 %
Lacerta vivipara	—0.42	90 %
Podarcis hispanica	—0.93	99.9 %
Podarcis muralis	—0.61	99 %
Psammodromus algirus	—0.74	99.9 %
Chalcides chalcides	—0.56	95 %
Coluber viridiflavus	—0.70	99 %
Coronella austriaca	—0.58	95 %
Coronella girondica	—0.79	99.9 %
Elaphe longissima	—0.67	99 %
Elaphe scalaris	—0.64	99 %
Malpolon monspessulanus	—0.71	99 %
Natrix maura	—0.64	99 %
Natrix natrix	—0.71	99 %
Vipera aspis	—0.62	99 %
Vipera latastei	—0.27	—
Vipera seoanei	—0.47	90 %

the northern side of the range and its fairly regular distribution in altitude.

As we have said, the amount of available surface in each altitude class is related to the expected numer of observations within it. So, we have done a similar correlation analysis for the area of an interval and the corresponding number of observations, and we have also estimated

the proportion of expected findings of each species in each altitude class (assuming a direct relation area/number of data), comparing then the expected figures with the observed ones.

Correlation between area and number of observations is also clear and marked. For 28 of the 37 species the signification level of correlation exceeds 99 %; three species, *Euproctus asper, Rana temporaria* and *Pelobates cultripes,* which have a rather irregular distribution, show a low correlation, positive but not significant. Notwithstanding that relation, the number of observations in each interval differs from the expected in a complete linear dependence. In 28 species (76 %) the discrepancy is significant, and we may conclude that, as we know, available area is not the only factor influencing distribution in altitude.

We have studied only the two discussed factors, altitude and available area. To distinguish between the influences of both factors we have examined partial correlations between them and the data, thus keeping one of the factors controlled while the other is allowed to change. To do so we cannot use SPEARMAN correlation coefficient, but there is another ordinal measure of correlation (KENDALL coefficient) which may be easily generalized in the form of partial and multiple correlation coeficients (SOKAL & ROHLF, 1969). This statistic has been estimated for every śpecies and group of species to examine the relations:

Altitude - Number of observations
Available surface - Number of observations
Altitude - Available surface

The results are shown in table 5 for the main taxonomic groups. The

TABLE 5

Partial ordinal correlation between number of observations, available area and altitude

Group	$T_{a.s.}$	$T_{s.a.}$
Urodela...............................	0.126	0.627
Anura	—0.014	0.681
Amphibians	0.120	0.655
Sauria................................	—0.094	0.816
Ophidia..............................	—0.084	0.797
Reptiles	—0.140	0.743

$T_{a.s.}$: Kendall's tau partial correlation coefficient between altitude and number of observations, keeping available surface controlled.
$T_{s.a.}$: The same coefficient, but now between available surface and number of observations, controlling for altitude.

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corresponding coefficients for every species are similar, although not so high.

In all instances correlation between available surface and number of observations, keeping the other variable fixed, is high and significative. That result may seem surprising, but, in itself, does not allow us to infer that altitude is not linked to the distribution of data. We may only conclude that effects of altitude are masked by other factors, as available surface. These factors affect the opportunity of observation both through activity of animals and human activity.

4. Results: Diversity

Diversity in a natural community reveals the point reached by evolutive pressures within it; these pressures work through mainly genetic mechanisms at the population level, and mainly ecological at the biocoenosis level; of course, both kind of mechanisms are strongly linked.

In all mountain areas, such as the Pyrenees, altitude is a very important factor in the evolution of organisms. Topography allows a large landscape and biotipe variety and, hence, many opportunities for adaptive evolution. Moreover, in mountain species the island structure of the peaks keeps many populations isolated, so helping genetic differentiation. The hard environmental conditions, while increasing selective pressures and favouring adaptation, simplify communities, which have few species, mainly of the pioneer type. Both factors give opposite influences on mountain ecosystem diversity, the simplifying factors being by far the strongest. Hence diversity must decrease with altitude, although in a mountain area it will always be larger than in a flat area of similar size, according with the result of several studies done. Moreover, human action increases this tendency, as observations are less likely in high mountain areas.

In this paper diversity has been estimated by three procedures (specific richness and SHANNON and BRILLOUIN estimates). Three levels of association measures have been used (nominal, ordinal and numeric), so nine analysis were done in all, giving similar results. Some of the results are presented in table 6.

As may be expected, diversity decreases with altitude. Specific richness is 34 species between 0 and 200 m., and is mantained about the same value to 1200 m.; from this altitude up it decreases; diversity has the same behaviour.

TABLE 6

Variation of diversity with altitude in pyrenean herpetocoenoses

Altitude (m.)	Diversity amphibians	Diversity reptiles	Joint diversity (bits/observation)
0-200	3.48	4.05	4.77
200-400	3.14	3.99	4.64
400-600	3.30	3.90	4.56
600-800	3.32	4.08	4.74
800-1000	3.20	3.88	4.54
1000-1200	3.11	3.88	4.50
1200-1400	2.96	3.43	4.15
1400-1600	2.51	2.90	3.63
1600-1800	2.35	2.20	3.50
1800-2000	2.34	2.79	3.46
2000-2200	2.21	2.59	3.22
2220-2400	1.89	2.06	2.87
2400-2600	1.37	0.92	2.16
2600-2800	0	0	1
2800-3000	0	0.92	0.92

In table 6 values of specific richness and diversity are shown for amphibians, reptiles and the whole of herpetofauna in each altitude class. Fig. 3 plots the data from the table, and reveals that variation of diversity with altitude is alike in amphibians and reptiles, and does not follow the hipsometry strictly. Thus, lowland areas show a diversity clearly higher than expected from the extension they have in the studied region.

We get fairly high diversity values, often over 4 bits observation. Values so high are considered indicative of heterogeneity in the sample, and in this instance, of course, there is heterogeneity, coming both from the large area of altitude intervals and from their varied features.

Diversity is consistently lower in amphibians than in reptiles. The former have less species in the Pyrenees, and also, being linked to water, have less opportunities of dispersion.

There is a moderate diversity maximum between 600 and 800 m. In that interval there are many Mediterranean biotopes (on the southern slope) where temperature and rainfall are adequate for thermophilous species, together with dense pine and beech forests, and even mountain biotopes, in cold and wet places. So, this altitude class has a greater variety of landscapes than others, and this is the reason for its higher diversity. Moreover, the area of this class is also the greatest. This interval may be described as an altitudinal ecotone which, of
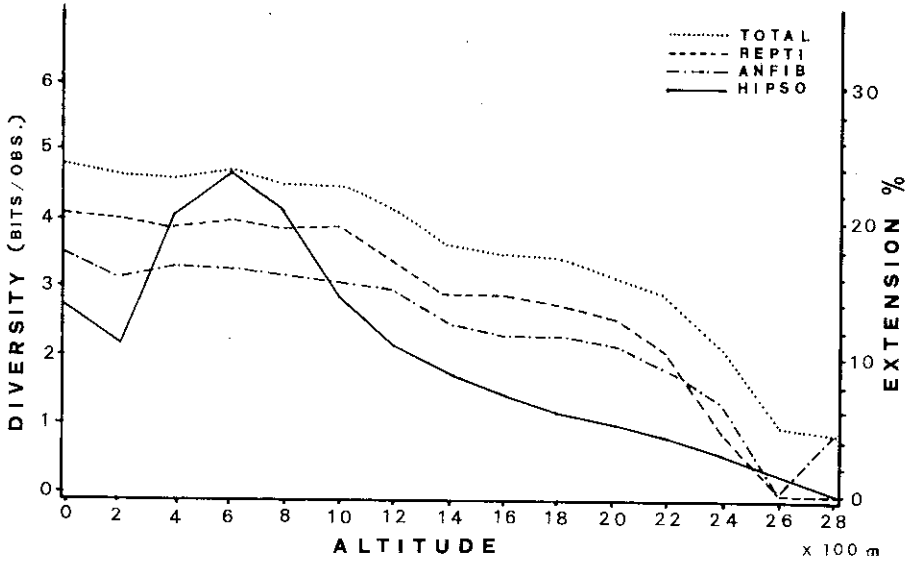
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Fig. 3.—The relations between diversity with specific richness of Pyrenean herpetofauna, and altitude with available surface in each altitudinal class. See table 7 for the mathematical expression of such relations. *(Relación entre la riqueza específica y la diversidad de la herpetofauna pirenaica, con la altitud y con la superficie disponible en cada intervalo altitudinal. Ver tabla 7 para las funciones que se ajustan a esta relación).*

course, goes up or down from some parts of Pyrenean territory to others.

Decreasing of diversity with altitude is neither constant nor regular, but, nevertheless, a linear model is still the best explanation among the several attempted models. The corresponding equation would be

$$Y = -0.00134\,X + 5.526$$

where Y is the diversity and X the altitude in meters. The correlation coefficient is fairly high, 0.929, and strongly significant (> 99.9 %). After that equation, diversity at sea level would be very high, over 5.5 bits/observation, and would decrease about 1.34 b/o for every 1000 m., that is, it would reach value 0 at 4130 m. Of course, there are no peaks over 3400 m., and herpetofauna disappears at about 3000 m; moreover maximum theoric diversity is 5.21 b/o, so diversity in lowland areas is less than expected from the linear model. These faults at the extremes are unsatisfactory, but for altitudes between 600 and 2800 m, that is, for over 70 % of studied area, linear model is satisfactory, and allow us to say that, between these altitudes, diversity decreases regularly as we go up.

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We have also studied the relation between diversity and area at each altitude interval. As everyone knows, diversity in a place grows with considered area until reaching saturation level. The idea of "minimal sampling area" is closely related to such a level of saturation, because, after reaching the minimal area, further large increases of it give only small increases in diversity or specific richness.

Theoric functional relation between area and diversity is of power type. If A is the considered area and E the number of species found within, we have

$$E = cA^k$$

where c is a constant related with diversity/unity of surface and k is another constant which indicates the relation between E and A.

For Pyrenean herpetofauna, data fit fairly well to a similar simple power model, with very high k, varying from 0.53 to 0.59 for different diversity estimates, and still higher for specific richness. This result shows the complexity of mountain areas, where increase in considered surface brings different ecosystems within, thus allowing a fast growing of diversity. This point will be further discussed later.

5. Results: affinity between species

Every studied species has some definite distribution of altitudinal data. Taking the observed distribution we can calculate some measure of similarity between those altitudes occupied by each pair of species. From the resulting similarity matrix, it is possible to derive, through ordinary clustering procedures, a classification scheme. Of course, the groups so obtained have a better basis than the ones derived from mean altitude only.

We have used ordinal correlation coefficients as similarity measures. After processing the data through a clustering program we obtained the next dendrogram (Fig. 4).

We can see that two main groups are clearly separated, the first one with 11 mountain species and the second with the 26 remaining species. Within the second we can distinguish a group of lowland species (18) from other of species with a broad distribution in altitude, and hence, rather tolerant. Within the larger subgroup, it is possible to separate, although not so clearly, a set of six thermophilous species, which seem linked to areas with concave relief (rivers, routes, human settlements and so on, normally localized in valleys), another group of two species of humid forests or meadows, and a last group of ten
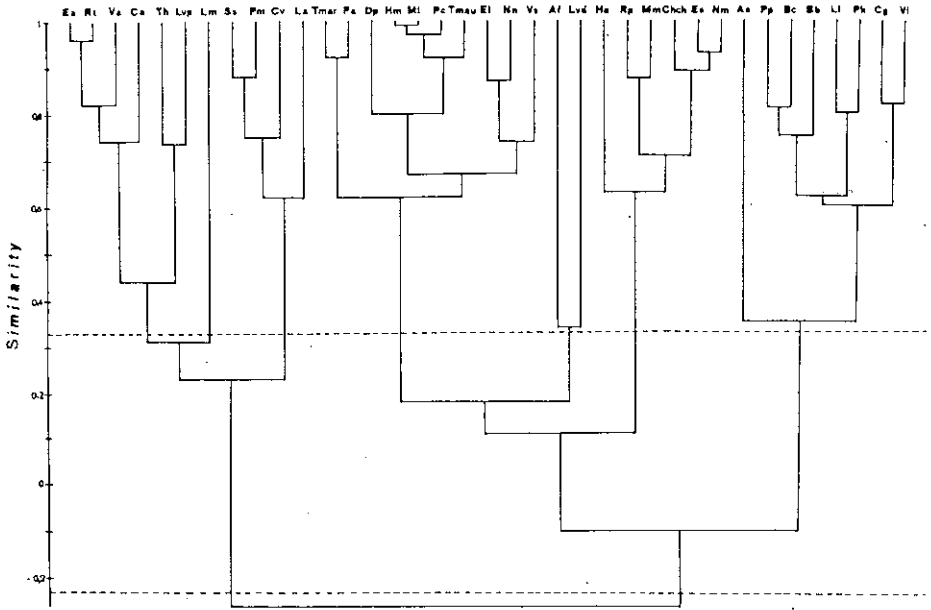
Fig. 4.--Classification of Pyrenean species of amphibians and reptiles, from their altitudinal distributions. The two vertical lines mark the similarity levels giving the different groups. *(Clasificación de las especies pirenaicas de anfibios y reptiles a partir de las respectivas distribuciones altitudinales. Las dos líneas verticales corresponden a los dos niveles de similaridad elegidos para la separación de los grupos).*

species from low altitude areas. As for the group of mountain species, there are two parts within, one with high mountain species and another with species living both at the top levels and in middle altitude forests.

The composition of these groups is listed next; it is worth insisting on the weight of the data from the southern Pyrenean slope in making the classification; that circumstance may produce perhaps inadequate names for some groups on the northern slope; there, as we have said, inhabit, at low altitudes, several species which, on the Spanish side, are montane.

1. High mountain species: *Euproctus asper, Triturus helveticus, Lacerta vivipara, Vipera aspis, Rana temporaria, Coronella austriaca, Lacerta monticola.*

2. Species from high and middle mountains: *Salamandra salamandra, Podarcis muralis, Coluber viridiflavus, Lacerta agilis.*

3. Lowland species: *Triturus marmoratus, Psammodromus algirus, Discoglossus spp., Hyla meridionalis, Mauremys leprosa, Pelobates*

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cultripes, Tarentola mauritanica, Elaphe longissima, Natrix natrix, Vipera seoanei.

4. Middle mountain hygrophilic species: *Anguis fragilis, Lacerta viridis.*

5. Thermophilic species, often linked to water: This group is rather difficult to define; within it there are water-living species, as *Rana perezi* or *Natrix maura,* other species living on grassy banks or in zones with water-loving vegetation *(Hyla arborea, Chalcides chalcides),* and other species *(Elaphe scalaris, Malpolon monspessulanus)* which do not live in the vicinity of water. Probably the group includes species inhabiting valleys and similar areas with negative relief. We have started a new paper where, with more data and considering also the spatial coordinates, it is possible to get estimates of laplacian (surface derivative) for several points, and to associate these estimates with the presence level of different species. Probably this group will then be clearly defined.

6. Tolerant species, with a broad altitudinal range: *Alytes obstetricans, Pelodytes punctatus, Bufo calamita, Bufo bufo, Lacerta lepida, Podarcis hispanica, Vipera latastei.* Two of the species of this group, *P. hispanica* and *Lacerta lepida* can be defined as eurihipsic only on the southern slope; on the northern side they are stenohipsic and restricted to low altitudes.

6. Discussion

Our results allow us to establish some general ideas about distribution in altitude of Pyrenean herpetofauna, notwithstanding the limitations of original data, which have no ecological or geographical information.

In different places in the text the broad altitudinal range of most species has been emphasized, and the extension and variety of the Pyrenean region was given as an explanation. This extension makes our results not quite comparable to those supplied by other authors in different mountain areas of southwest Europe (FONS, 1975; LIVET & BONS, 1981; PÉREZ MELLADO, 1983; BAS, 1984; PLEGUEZUELOS, 1986 and 1987; DELIBES & SALVADOR, 1986, etc.). In spite of that, and with the indicated limitations (mainly that of restricting the application of results to the southern Pyrenean slope), these may be considered valid.

Three species called by FONS (1975) strictly montane, and which he normally found over 1800 m. *(Lacerta agilis, Lacerta vivipara* and *Coronella austriaca),* belong also to the group of high mountain species

of this paper, although the mean altitude for that group is less here than in FONS.

Many details gathered in figure 2, where species are ranked by mean altitude, agree with those supplied by PÉREZ MELLADO (1983) for the species common to both papers, in spite of the narrower altitude range of the area studied by that author; in both papers *Lacerta monticola* seems to be a peculiar species, restricted to top levels and with a small dispersion in altitude; *Bufo bufo* is a tolerant species both in Salamanca and in the Pyrenees, with a number of observations rather similar at different levels; *Mauremys leprosa* is restricted to the lowest areas; *Vipera latastei* is a middle-mountain species in both areas, and so on. In general, the ranking in altitude of common species is rather similar in both papers, in spite of metodological differences.

Also the groups defined by LIVET & BONS (1981): species stenohipsic from low altitudes, stenohipsic montane species and eurihipsic species, reveal themselves in the results of the present paper. The three species given by LIVET & BONS as montane *(Vipera aspis, Coronella austriaca* and *Lacerta vivipara)* are included here in the group of high mountain species.

All summarizing, although we have worked without ecological data, the obtained results are reliable, confirmed by other authors and allowing an ecological interpretation; as we have said, "the large numbers law" dilutes anomalies and partially compensates for the heterogeneity of data. But, of course, never can a set of randomly gathered data, taken for other objectives, be substituted for a sampling work well designed and well done.

The number of observations decreases with altitude, not only in the Pyrenees, but also, not surprisingly, in other zones studied by different authors. As far as we know, in no paper among the previously referred is the study of functional relationship between altitude and number of data attempted, nor is considered the importance of available surface in the gathering of a greater or smaller number of data. PÉREZ MELLADO (1983), however, takes a similar approach, when he compares the altitude distribution of observations in Salamanca with the hipsometry of that province, given by the altitudes of capture localities. In his paper are reported significative differences between observations and hipso-metry only for a few species; if not equivalent to a formal correlation, this result suggests at least the existence of a relationship.

A specific form of that relationship has been studied in the present paper, without arriving at interesting conclusions; the fit arrived at is good only for artificial functions; thus, these functions are named without commentary in table 7. Anyway, the number of observations

TABLE 7

Best fit models of regression for observations of pyrenean amphibians and reptiles

Related variables	Best fit model	Linear model	Power model
a) Pyrenees: Specific richness:			
Observations-altitude	$Y = 37/(1 + 3.07 \times 10^{-2} \times e^{0.002 \cdot x})$	$Y = -0.013X + 40.82$	$Y = 2243.5X^{-0.707}$
Observations-extension	$Y = 38.62 \times (1 - e^{-0.0003x})$	$Y = 0.005X + 5.97$	$Y = 0.036X^{0.8}$
b) Pyrenees: Diversity:			
Observations-altitude	$Y = 1.34 \times 10^{-3}X + 5.53$	$Y = 1.34 \times 10^{-3}X + 5.53$	$Y = 40.43X^{-0.362}$
Observations-extension	$Y = 5.54X/(11.5 + X)$	$Y = 4.89 \times 10^{-4}X + 2.02$	$Y = 0.117X^{0.433}$
c) South Spain Ranges: Specific richness:			
Observations-altitude	$Y = 17/(1 + 5.23 \times 10^{-2} \times e^{0.002X})$	$Y = 5.25 \times 10^{-3}X + 17.16$	$Y = 1471.-6X^{-0.774}$

follows hipsometry rather well (linear correlation coefficients of 0.856 for amphibians and 0.976 for reptiles). This is in agreement with the former conclusion concerning the masking of effects of altitude by the available area, or by other factors linked to the prospection effort. It must be pointed out, moreover, that other authors (PLEGUEZUELOS, 1987; BAS, in litt.) recognize a constant relation between altitude and the number of observations, independently of prospection effort.

Probably the most interesting subject in the present paper is the relationship between herpetofauna diversity and altitude or available area. This subject has a long history in plant ecology, with publications as old as 1859. Papers studying the relation of herpetofauna diversity with altitude are not so common, and more recent.

LIVET & BONS (1981) point out the stability of herpetofauna diversity between 100 and 1000 m. in Montagne Noire (Languedoc). This result agrees with our own conclusions for the Pyrenees: diversity remains stable below 1200 m. and decreases in the upper levels. The diversity values given by French authors are too low (1.05 to 1.99), and do not compare with our values (over 4 b/o). The reason for this difference is an improper use of logarithms: although LIVET & BONS calculate diversity by means of the SHANNON-WEAVER formula, they do not use binary logarithms but neperian ones. Besides that, diversity in Montagne Noire is objectively less than in the Pyrenees, as the area of the former is 130 times smaller. In Montagne Noire specific richness drops abruptly from 900 m. up, while in the Pyrenees the diversity drop is gradual and regular over 1200 m. This is probably also a consequence of different methodologies, but as methods of work are not clearly specified in the referred paper, the issue is open.

PLEGUEZUELOS (1986) studies distribution in altitude of amphibians and reptiles in the mountain ranges of southern Spain, using a sound sampling scheme, and he finds that, as expected, specific richness and diversity decrease with altitude. Although the form of this relation is not specified, it can be calculated from his data, being aproximately linear (see table 7). In his area the number of species remains rather stable until 1400 m., and decreases regularly from this altitude up, until 3000 m.; the result is, then comparable to our own findings.

Comparison of our results with those from DELIBES & SALVADOR (1986) is difficult, because these authors work only with a family of reptiles *(lacertidae)* and in a restricted altitudinal range (900-1700 m.). According to their paper, diversity decreases also regularly with altitude, having a local maximum at 1200 m.

The relationship between available surface and diversity has been far better studied than the one between altitude and diversity. Ideas

which are now well within the frame of general ecology (such as that of "minimal area") and even broad theories (such as island biogeography) have their roots in that relationship. In this field, people work normally with well defined and separate spatial unities, while in the present paper we use the area of different altitude classes, not so well delimited and with no separation at all.

The relation generally accepted is of power type, after the model initially proposed by ARRHENIUS (1921), and expressed by the formula

$$E = c A^k$$

where c and k are some constants; this model has been applied by many authors to vegetation of different territories, and by not so many to several animal groups (WILLIAMS, 1964; DIAMOND, 1972); MC ARTHUR & WILSON, 1967, and so on).

In 1943, WILLIAMS, in his paper with FISHER and CORBET, proposed a derivation of ARRHENIUS formula, together with a diagram which he himself made more comprehensive and detailed in his 1964 book. In this diagram, the relation species number/area was plotted in logarithmic scale for 273 studied areas, and considering only flowering plants. Within the figure, three parts can be separated by means of the different mean slope of fitted line; in the first of these parts diversity increases with the encompassed area until it arrives at some constant level, the so called "minimal area", between 10 and 1000 m.^{2}; in the second part, diversity also increases with area, but with a higher slope; values of k in the ARRHENIUS formula would be .15 to .3 in the first part, while in the second one, corresponding to larger territories (between 1 ha and 10^6 Km^2) values are .3 to .4. The reason is the heterogeneity of larger areas, where the effects of area increase are added to those of inclusion of different natural communities.

According to their respective extensions, the areas considered in the present paper would be similar to those of the second part of WILLIAMS scheme, and hence, would have a similar slope (that is, a similar value of k) would be expected. That slope has been found, in fact, for the herpetofauna of Caribbean islands (MC ARTHUR & WILSON, 1967), and could be therefore expected in the Pyrenean herpetofauna. But the slope derived from our data is clearly higher, .79, similar to mean slope in the third part of WILLIAMS drawing. This part includes territories with an area of over 10^6 Km^2, where to the effects of increase in extension and multiple ecosystems, other effects must be added, such as those derived from joining areas with a very different biogeographic and evolutive history.

From the preceding lines we can conclude that, in the Pyrenees,

variation of herpetofaunistic diversity with altitude is a consequence of diverse, but related, factors: decrease of available surface in the top altitude classes; uniformization of communities by hardness of environmental conditions; the part played by the mountains as a more or less permeable barrier in relation to faunas of diverse origin (Eurosiberian, Mediterranean, Iberian...), and so on.

This multiplicity of factors has also been given as a reason to explain the inverse relation between diversity and altitude in other animal groups (birds in the Andes of Colombia and Ecuador: VILLEUMIER, 1970; birds in New Guinea mountains: DIAMOND, 1972; birds in Mount Ventoux: BLONDEL, 1978, and so). After these papers, in addition to listed factors, others may be considered, such as the isolation level of considered territories, or other biogeographic circumstances whose effects are, at times, opposite to those of main factors; that is, enrichment of natural communities with altitude is quite possible, at least in tropical mountains.

7.   Conclusions

An adequate study of distribution of animals along altitude gradients requires, no doubt, proper data, gathered with well planned samplings, and with the objetive of such a study in mind. Nevertheless, these data cannot always be taken. Otherwise, it is easy to have plenty of conserved material coming from some limited area, and with the possibility of establishing the altitude of capture data. Many collections within museums or research institutes can serve, therefore, as sources of data.

The main purpose of this paper is to point out the usefulness of that type of incomplete data, which after being analyzed, may reveal several interesting biogeographic details and patterns, and suggest ideas about the evolution of communities within the studied zone. Here we have commented, rather briefly, on some of the results derived from the simplest analysis of a sample of altitudes, corresponding to capture localities of 37 Pyrenean species of amphibians and reptiles. A more complete study can be found in REINE (1985).

There is another conclusion of our work, dealing with the heterogeneity of data. In animals as dependent on environmental conditions as are amphibians and reptiles, there are many factors patterning the distribution; altitude integrates only some of these. To re-emphasize the great variety of Pyrenean region, with the intricate

network of Atlantic, Mediterranean, continental or montane zones, and the complex biogeographic history of pass, migration, area expansion or retraction, and so on, is also, of course, an important consequence of this paper.

Observation opportunities of an animal decrease in altitude, because of the smaller area and harder accesibility of top levels; moreover, mountain communities are impoverished as we go up, both in species and individuals; that leads to a negative relation between abundance or diversity of an herpetofauna and the mean altitude of its biotope, a relation which is well illustrated by a linear compound function. In the Pyrenees, the function is made up of two parts -the first one corresponding to lower levels, where regression slope is small, and the second to the levels of over 1200 m., where decrease of abundance and diversity is rather abrupt. A similar relationship is found by other authors in different mountain ranges and with different animal groups.

In conclusion, this paper points out the direction that a more detailed research should take: with a not so uneven and more comprehensive database, which is now on the making; with a methodic organization of sampling work, and with a degree of independence in different areas, each of them more ecologically uniform. That research would allow, no doubt, not only more sound conclusions, but also consideration of other aspects which we have been unable to deal with here (taking into account, for instance, spatial relations between data). But, although this work is needed, and will be done, we think that its conclusions will not disagree with those in the present paper.

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