Doñana, Acta Vertebrata, 4: 27-34, 1977.

Species densities of Reptiles and Amphibians on the Iberian Peninsula

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A century ago in a now classic work on tropical biology, Wallace (1878) discussed geographical patterns in numbers of species (also termed "species richness" or "species density"). He noted the now much celebrated phenomenon that species richness of most plant and animal groups tends to increase towards lower latitudes. So-called latitudinal gradients in diversity have since been well documented (Fisher, 1960; Simpson, 1964; Pianka, 1967; Cook, 1969; Kiester, 1971; Schall and Pianka, 1977). Speculation as to possible causes of these widespread patterns abounds (Pianka, 1966).

Terentev (1963) and Simpson (1964) independently devoloped a simple yet powerful technique for analysis of geographical patterns in numbers of species. They partitioned maps of large landforms into equal-sized quadrates and used range maps of individual species to stimate the numbers of species occurring at different areas (this technique thus lumps the between-habitat and the within-habitat components of species diversity). As reliable range maps became available these methods were applied to various vertebrate taxa in North America, South America and Australia (Simpson, 1964; Cook, 1969; Kiester, 1971; Roig and Contreras, 1975; Rogers, 1976; Pianka and Schall, 1978; Schall and Pianka, 1978). Here we exploit this technique to analyze geographical patterns in the species richness of reptiles and amphibians on the Iberian peninsula using the range maps of Salvador (1974). Correlations between species densities of various taxa and long-term average climatic conditions provide insights into why these patterns occur.

Methods

Degree meridians of latitude and longitude were used to partition the Iberian peninsula into 81 quadrates, each 1° of latitude by 1° of longitude. A transparent overlay was superimposed on each range map and the numbers of species of frogs and toads, salamanders, turtles and tortoises, lizards, and snakes tallied for each square. Our analysis is based on the geographic distributions of 36 species of reptiles (13 snakes, 19 lizards and 4 turtles) and 21 species of amphibians (8 salamanders and 13 frogs and toads).

Estimates of the following five climatic measures were also made for each degree square using the maps of ESCARDO (1970): average annual precipitation (Ppt), average annual hours of sunshine (Sun), average July temperature (Temp), difference between the mean temperature of the warmest and coldest month (Diff), and the mean duration of the frost-free period (FF), an estimate of the length of the growing season.

A correlation analysis was performed on the species densities of various herpetological taxa, the above five climatic variables, and latitude and longitude. In addition, we used stepwise multiple regression to order environmental variables by the degree to which they reduce residual variance is species densities.

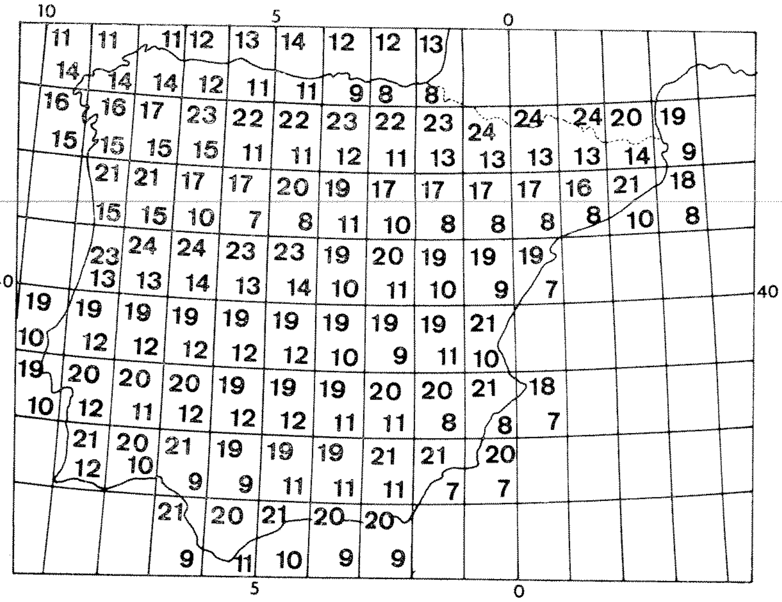

Fig. 1. Numbers of species of reptiles (upper number in each box) and amphibians (lower number) occuting in each one degree square grid on the Iberian peninsula.

Results and Discussion

Figure 1 shows the numbers of species of reptiles and amphibians that occur in each quadrate. Hours of sunshine and mean July temperature both decrease markedly with increasing latitude, whereas average annual precipitation *increases* fairly strongly towards the highest latitudes (upper panel of Figure 2). However latitudinal gradients in species numbers are slight or nonexistent over most of the peninsula (lower panel of Figure 2). At the

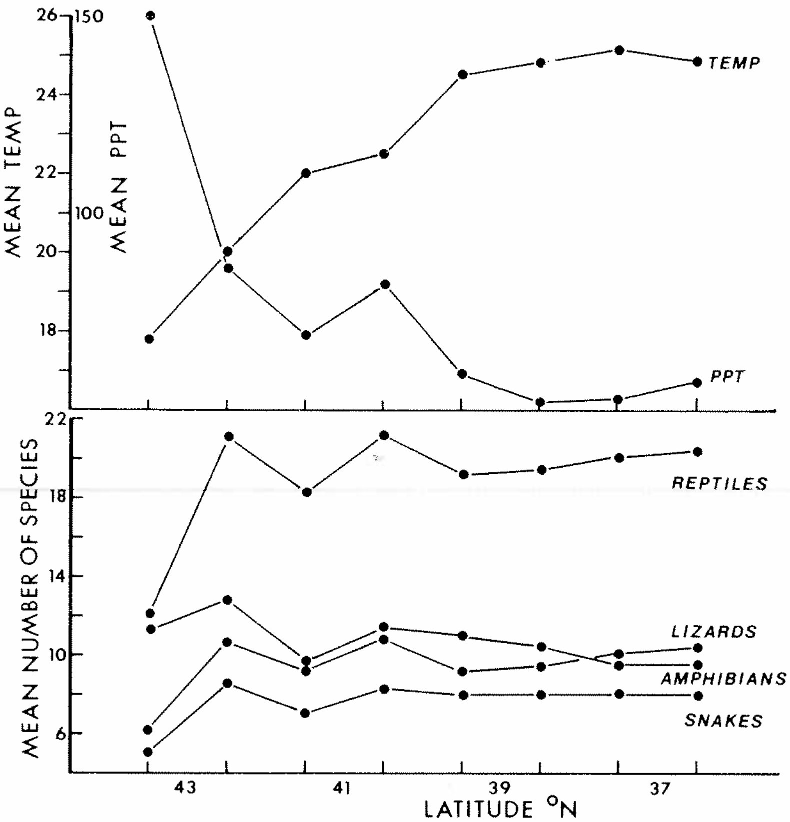

Fig. 2. Above: Mean July temperature (Temp) and mean annual precipitation (Ppt) plotted against latitude. Below: Mean species density for several herpetological taxa plotted against latitude. Means for climatic variables and species densities computed by averaging over all quadrates within a degree of latitude.

far northern edge of Spain, diversity drops off fairly steeply for reptiles (Figure 2). Iberian lizards do not increase in numbers of species over 8 degrees of latitude; over the same latitudinal range in the United States, lizard species density increases 3.3 X (Figure 3) and over 18° latitude mean lizard species number increases 14 fold in North America (SCHALL and PIANKA, 1978). Amphibians, particularly salamanders, increase towards the west (Table 1) Amphibians and reptiles differ in the signs of their correlations with latitude and most climatic variables (Table 1). As might be expected, amphibians species densities (especially salamanders) vary positively with annual precipitation, but negatively with mean July temperature and hours of sunshine. In

Table 1

Simple product-moment correlation coefficients between various taxa and physical variables.

Taxonomic Group	Latitude	Longitude	Ppt	Sun	Temp	Dif	FF
Turtles	—.59*	—.29	—.66*	.76*	.63*	42*	.07
Lizard	—.24	.03	—.29	.47*	.06	.29	—.19
Snakes	—.37*	—.26	—.32*	.49*	.40*	.38*	—.07
All Reptiles	—.39*	—.13	—.41*	.60*	.29	.40*	—.14
Frogs & Toads	.18	.36*	.23	—.04	—.33*	.05	—.19
Salamanders	.35*	.55*	.61*	—.39*	—.25*	—.26	—.05
All Amphibians	.30*	.51*	.47*	—.24	—.47*	—.12	—.13

* =Correlation significant at the P<.01 level.

contrast, all reptile groups correlate negatively with precipitation and positively with temperature and sunshine. North American and Australian reptiles and amphibians show similar trends (ROGERS, 1976; SCHALL and PIANKA, 1978; PIANKA and SCHALL, 1978).

In Table 2 stepwise regressions order climatic variables by the degree to which they reduce residual variance in species densities of reptiles, lizards, and amphibians Approximately a third to a half of the variance in species

Table 2

Stepwise regression using reptile, lizard, or amphibian species density as the dependent variable and five climatic measures as independent variables. Variables are listed in order of their contribution to reduction in residual variance in species numbers, Variables are listed only if they reduced residual variance significantly when added to the equation.

Taxon	Rank	Variable	Cumulative r^2	Significance
Reptiles	1	Sun	.355	<.001
	2	FF	.472	<.001
	3	Temp	.506	<.05
Lizards	1	Sun	.215	<.001
	2	Temp	.418	<.001
	3	FF	.493	<.001
Amphibians	1	Temp	.227	<.001
	3	Ppt	.268	<.05
	3	Sun	.343	<.05

numbers is accounted for by the significant variables. Comparing Tables 1 and 2, lizards and reptiles have diversified in sunny, warm places whereas amphibians have done so in cool, wet zones.

In accounting for a similar pattern for North American and Australian lizards, we proposed that sunfall is critical for ectothermic lizards to maintain predictably high body temperatures (SCHALL and PIANKA, 1978). In predictably sunny environments it is inexpensive for lizards to maintain high body temperatures, allowing resource specialization and increased numbers of species in the community.

In North America, climatic factors reduce residual variance in lizard species density by a full 84% (SCHALL and PIANKA, 1978). The figure for Australian lizards is only 22% (SCHALL and PIANKA, 1978), whereas Iberian lizards are intermediate (49 %, Table 2). These results could indicate the relative extent of ecological divergence among the lizard species of each of the three continental regions. Australian lizards are exceedingly diverse in both numbers of species (over three times the number in the United States) and in the range of ecological niches they exploit. In addition to a rich fauna of fairly typical lizards, these include small nearly legless subterranean skinks (*Lerista*), snake-like pygopodids and very intelligent large mammal-like varanid lizards. The Iberian peninsula is about 9 % the area of the continental United States (81 1° by 1° quadrates versus 895 in the United States) and yet supports 19% of the number of lizard species: hence twice the overall species richness. We selected 81 North American squares at latitudes identical to those of Iberia, in areas with similar sunfall (western USA) or similar precipitation levels (central USA). In both sets of North American quadrates, the mean number of species of lizards was about 5.4 compared with an aver-

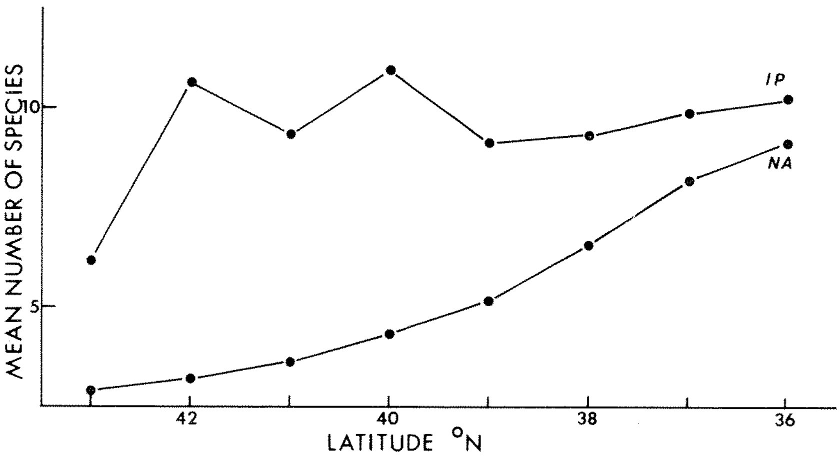

Fig. 3. Average species density of lizards in one degree squares versus latitude on the Iberian peninsula (upper line) and on the North American continent (lower line).

age species density of 9.5 in all quadrates of the Iberian peninsula. Thus the lizard fauna of the Iberian peninsula is roughly twice as rich in species as areas at comparable latitudes in North America. At low latitudes, however, lizard faunas of the two areas are roughly similar (Figure 3).

Taxonomic complementarity, defined as an inverse correlation between the species densities of two taxa, does not occur among the Iberian herpetofauna except between turtles and salamanders ($r = -.50$) and between turtles and all amphibians ($r = -.32$). Such patterns are probably not due to competition between higher taxa but rather simply reflect diversification of various taxa in environments that favor their particular body plan and ecological strategy. Salamanders compete with frog larvae, for example, and yet their species densities are positively correlated in Iberia ($r = .58$).

Conclusions

Intercontinental comparisons of species density patterns reveal both similarities and intriguing differences. The herpetofauna of the Iberian peninsula shows similarities to North America and Australia in that (1) reptiles are negatively correlated with precipitation and positively with temperature and sunshine; (2) sunfall appears the critical factor involved in lizard species diversification; (3) amphibians are most diverse in cool, wet zones.

In contrast to North America, there are no Iberian latitudinal trends in species numbers despite such trends in climatic factors. The peninsula has an intermediate lizard species richness compared with North America and Australia and the proportion of variation in lizard species numbers accounted for by climatic factors is also intermediate. An apparent negative relationship between species richness and proportion of variance reduced could be a statistical artifact or reflect real differences in ecological diversity among the three continents. This kind of analysis can be extended as reliable range maps for other taxa and geographic areas become available.

Acknowledgments

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Resumen

Se estudió la distribución del número de especies (densidad de especies) de lagartos, tortugas, serpientes, anuros y salamandras en la península Ibérica utilizando 81 cuadrantes de 1° de latitud por 1° de longitud. La densidad de especies pertenecientes a la herpetofauna permanece constante aunque la temperatura y la precipitación cambian con la latitud. La riqueza de especies de anfibios es mayor en zonas frías y húmedas, mientras que la mayor densidad de especies de reptiles aparece en regiones áridas, soleadas y cálidas. La fauna ibérica de lagartos parece ocupar un lugar intermedio en cuanto a la riqueza de especies y quizás en cuanto a la diversificación ecológica, cuando se la compara con la poca riqueza de Norteamérica y la gran riqueza de Australia.

Summary

Numbers of species (species density) of lizards, turtles, snakes, anurans, and salamanders were tallied for 81 1° of latitude by 1° of longitude quadrates on the Iberian peninsula. Although important climatic variables such as temperature and precipitation change with latitude, species densities of the herperofauna do not. Amphibian species richness is highest in wet cool zones, whereas reptiles reach highest species densities in arid hot sunny regions. The Iberian lizard fauna appears roughly intermediate in relative species richness and perhaps ecological diversification compared to North America (low richness) and Australia (high richness).

References

COOK, R. E. (1969): Variation in species density in North American birds. *Systematic Zoology* 18:63-84.

ESCARDO, A. L. (1970): The climate of the Iberian peninsula. Chapter 5 (Pages 195-239) *in*: C. C., Wallen, ed., *Climates of Northern and Western Europe.* World Survey of Climatology, Volume 5. El sevier, Amsterdam.

FISCHER, A. G. (1960): Latitudinal variation in organic diversity. *Evolution* 14:64-81.

KIESTER, A. R. (1971): Species density of North American amphibians and reptiles. *Systematic Zoology* 20:127-137.

PIANKA, E. R. (1966): Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100:33-46.

— (1967): On lizard species diversity: North American flatland deserts. *Ecology* 48:333-350.

— and J. J. SCHALL (1978): Species densities of terrestrial vertebrates in Australia. Chapter in: A. Keast, ed., *Ecological Biogeography in Australia* D. W. Junk, The Hague.

ROGERS, J S. (1976): Species density and taxonomic diversity of Texas amphibians and reptiles. *Systematic Zoology* 25:26-40.

ROIG, V. G. and J. R. CONTRERAS (1975): Aportes ecológicos para la biogeografía de la provincia de Mendoza *Ecosur* 2: 185-217.

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ESCARDO, A. L. (1970): The climate of the Iberian peninsula. Chapter 5 (Pages 195-239) *in*: C. C., Wallen, ed., *Climates of Northern and Western Europe.* World Survey of Climatology, Volume 5. El sevier, Amsterdam.

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KIESTER, A. R. (1971): Species density of North American amphibians and reptiles. *Systematic Zoology* 20:127-137.

PIANKA, E. R. (1966): Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100:33-46.

— (1967): On lizard species diversity: North American flatland deserts. *Ecology* 48:333-350.

— and J. J. SCHALL (1978): Species densities of terrestrial vertebrates in Australia. Chapter in: A. Keast, ed., *Ecological Biogeography in Australia* D. W. Junk, The Hague.

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ROIG, V. G. and J. R. CONTRERAS (1975): Aportes ecológicos para la biogeografía de la provincia de Mendoza *Ecosur* 2: 185-217.

SALVADOR, A. (1974): *Guia de los Anfibios y Reptiles Españoles.* ICONA. Madrid.