

Ecological study of the Clubionoidea and Thomisoidea (Araneae) in the Spanish Central System

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Résumé

Cette étude fut réalisée au cours des années 1981, 1982 et 1983; elle porte sur les araignées Clubionoidea et Thomisoidea des régions centrale et occidentale du Système Central espagnol. On a sélectionné 118 stations d'échantillonnage dans lesquelles les araignées ont été prélevées par différentes méthodes d'échantillonnage complémentaires: fauchage de la végétation et chasse à vue pendant un temps déterminé, prélèvement de la litière et pièges d'interception (pit-fall).

On a prélevé 90 espèces parmi lesquelles 26 sont sporadiques. Dans la région étudiée, le printemps est la saison de l'année où l'on trouve les adultes actifs d'un très grand nombre d'espèces.

La considération du milieu comme un ensemble de facteurs d'actions isolées est plus ou moins arbitraire, car la distribution et l'activité des organismes dépendent de l'ensemble des variables du milieu. Cependant, cette considération permet de mettre en relief la relation entre l'intensité des facteurs choisis (végétation, altitude et continentalité, dans ce cas) et la présence et l'activité des organismes ainsi que les réactions communes de certaines espèces face à des conditions de vie semblables (tout en détachant l'existence de groupes d'espèces avec un comportement similaire par rapport aux facteurs du milieu). L'information mutuelle représente donc une méthode analytique très appropriée pour l'étude de l'écologie des araignées.

Enfin, cette étude s'achève avec une étude d'ensemble des communautés d'araignées afin de mettre en relief leurs relations avec les différents facteurs du milieu. Pour ceci, on a utilisé l'analyse des correspondances.

A partir d'une analyse générale de l'ensemble des données, dans laquelle les relations existantes avec la végétation se manifestent essentiellement à travers des gradients d'humidité et d'insolation, on a réalisé plusieurs analyses partielles.

Les chênaies (formations de *Quercus pyrenaica* Willd.) et les pâturages de la classe *Arrhenatheretea* se détachent à cause de leur richesse spécifique très élevée; dans les premières, le mésoclimat est un facteur déterminant de la composition des communautés d'araignées: il proportionne une division macroscopique en accord avec l'exposition (nord et sud) des deux versants étudiés; dans les pâturages, c'est le microclimat qui s'impose, et ceci accentue l'intérêt des caractéristiques locales. On a également observé l'habitat «sous les pierres»: la particularité de cet habitat se manifeste par la composition spécifique très différente des autres.

Summary

An investigation was made over a three-year period (1981-1983) of the Clubionoidea and Thomisoidea inhabiting the central and western part of the Spanish Central System. 118 sampling sites were chosen in which the spiders were captured by different complementary sampling methods; these were: a sweeping through the vegetation over a predetermined time, visual capture over a given time, collection of forest floor, and pit-fall traps.

Ninety species were found, of which 26 were sporadic. In the zone studied, spring was found to be the season showing the presence of active adults of the greatest number of species.

Consideration of the environment as a set of factors acting independently is more or less arbitrary owing to the fact that the distribution and activity of living organisms depend on the set of variables present in the environment. However, such a consideration does serve to show up the relationship between the intensity of the factors selected (in case, vegetation, altitude, and continentality) and the presence and activity of the organisms, together with the relationships common to certain species to the same environmental conditions (notably the existence of groups of species that respond similarly to environmental factors). Accordingly, such mutual information may constitute a very appropriate analytical method in the study of the ecology of spiders.

This paper reach completion in an attempt to relate spider communities to environmental factors. To do so, the reciprocal averaging technique is employed. From a general analysis of all the data which shows the relationships between the communities and vegetation, though mainly through humidity and sunshine gradients, different partial analyses are carried out. In particular, oak groves (*Quercus pyrenaica* Willd. formations) and grasslands composed of the class *Arrhenatheretea*, were considered owing to their great richness in species; whereas in the former the mesoclimate is determinant in the composition of the spider communities, providing a macroscopic division in accordance with the exposure (N and S) of the two large mountain sides studied, in the second case the microclimate is overwhelming, which enhances the interest in local characteristics. The «under stone» habitat was also studied; this reveals a certain peculiarity in species composition compared with the other enclaves.

I. HABITAT AND SPECIES

Introduction

In the ecological study of spiders, a good knowledge of their taxonomy is essential; without it the establishment of specific structures, the comparison between populations and the search for interspecies relationships is evidently impossible (TURNBULL, 1973; DONDALE, 1975; CHRISTOPHE & al., 1979). However, the integral study of the order Araneae in the Spain today is not a simple matter owing to the difficulty involved in the determination of most species; this is due to the lack of keys for the Iberian arachnid fauna, which is very rich and shows certain peculiarities when compared with those from central and north European areas, which have been studied in greater depth. This difficulty is enhanced by the small size of the specimens, the problems inherent in capturing adults (necessary in most cases for a correct determination at species level) and because of the colonization of all imaginable habitats, which in turn hampers the search itself for specimens.

Accordingly, in the present study we decided to focus our attention on only one group of taxonomically related families: the Clubionoidea and Thomisoidea spiders (families Anyphaenidae, Clubionidae, Sparassidae and Zoridae, and Philodromidae and Thomisidae, respectively) whose systematic structuring, currently very controversial, has already been discussed (BARRIENTOS & URONES, 1985).

For the study, a geographic region was chosen which has an ecotone character (*Durilignosa-Aestilignosa*) and that is situated between the Mediterranean region and

the Eurosiberian region with a view to being able to start the search for the dominant ecological variables in species distribution.

In this part, we shall focus attention on the basic aspect of the territory studied, the sampling methods and the qualitative study of the species collected. The second part will deal with the role of certain environmental factors regarding the distribution of the spider species and the third part will offer a synecological study of the spider communities, attempting to relate them to the different ecological factors.

The environment

1. General characteristics

The territory studied covers the central and western parts of the Spanish Central System, a mountain chain which acts as a dividing line between the Duero and Tajo basins. This territory corresponds roughly to $40^{\circ}01'$ and $40^{\circ}40'$ N and $5^{\circ}00'$ and $6^{\circ}52'$ W (the Portuguese border) and includes a wide range of altitude in which the most extreme points are about 250 m above sea level as minimum (the banks of the river Tiétar, an affluent of the Tajo) and 2592 m a.s.l. as maximum (at Pico Almanzor in the Gredos Sierra). The area is included in three administrative provinces: Avila, Cáceres and Salamanca (fig. 1).

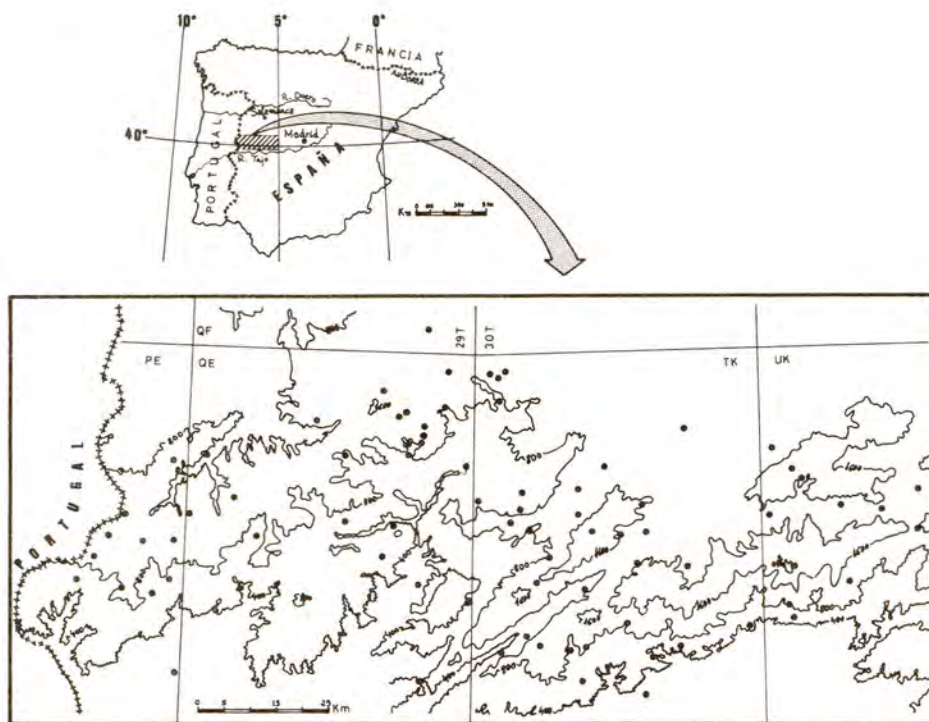


Figure 1. — Situation of the territory studied and of the 76 geographic localities including the 118 sampling sites.

Regarding *geology*, the territory lies within the Central-Iberian zone of the Hesperian massif, and has a predominantly siliceous lithology.

In the broad sense of the term, the *climate* of the area is fairly homogeneous; in the middle and low zones it corresponds to a humid mediterranean climate, almost semi-arid in the NE and at the summits it has a typical high mountain climate (ALLUE ANDRADE, 1966; FONT TULLOT, 1983).

According to FONT TULLOT (1983, p.22) the mean annual temperature ranges between less than 8°C at the summits and 16°C at certain sites to the north of the province of Cáceres. Regarding annual rainfall, according to the same author (FONT TULLOT, 1983, p.75) the maximum corresponds to Béjar-Gredos massif (between 1500 and 2000 mm), although practically the whole zone receives more than 700 mm annually.

With respect to the *vegetation*, the Central System is situated in overall terms in the Mediterranean Region, though also exhibits certain characteristics of the Nemo-ral Eurosiberian Region, sometimes due to the altitude of certain westernmost sectors, where the effect of oceanic winds can be felt. According to its coordinates, the area should show a sclerophile vegetation but its altitudes mean that the marscescence phenomenon exists as well as the presence of deciduous vegetation. On the other hand, the proximity of the ocean leads to the presence of characteristic fruticose formations. All this results in a wide variety of different types of vegetation, from large forests to cacuminal swards, including grasslands and bush formations.

2. Sampling sites

Owing to the extension and heterogeneity of the area, only representative samples were collected. The sites where they were taken from were chosen according to an oriented selection; that is, taking the most representative emplacements of the set from the zone delimited in order to obtain a true reflexion of its spider population. An attempt was made to cover the whole altitude gradient and most of plant formations; we also tried to cover the area uniformly in the sampling procedure.

Each sampling site has a uniform type of vegetation, catalogued according to phytosociological terminology using class ranks and only in a few cases resorting to the alliance rank. Determination of the plant groups was performed by Dr. E. RICO of Department of Botany of the University of Salamanca.

A total of 118 sites belonging to 76 geographic localities were visited (fig. 1). These sites were characterized according to their UTM coordinates, altitude, the river basin to which they belong and the type of vegetation. The sites were sampled regularly during 1981, 1982, and 1983.

Material and methods

1. Collection

Since we were interested in only part of the spider community in this study (the taxocenosis *Clubionoidea* and *Thomisoidea*), several different and complementary capture methods were chosen with a view to obtaining the representation of the greatest number of species. The methods employed were:

Sweeping of different plant substrates for unit period of time using a sweep-net (of resistant material, 35 cm diameter and 70 cm depth with a 50 cm handle for grassy zones and 80 cm for bushy and tree zones) over a period of 30 min. The contents of the net were tipped onto an 80 × 80 cm white cloth and the spiders were collected by placing a glass tube along the direction of their movement or using a pooter.

Regular collecting visits were made to the stations over the three year study period.

Hand collecting for unit period of time: this involved capturing all the spiders the observer could see over 30 min either on the ground, under stones and barks, and in sac retreats, etc. Sampling was carried out regularly at all the sites over the three years.

Collection of forest floor: occasionally, during the study period, the litter was collected in 20 × 30 cm plastic bags; afterwards in the laboratory the spiders were taken from the contents, spread onto a white illuminated surface, using a pooter.

Pitfall traps: for this method, 9 × 13 cm plastic cup traps were used containing 2% formalin and, exceptionally, white wine. A flat stone was placed over the cups and supported by a tripod of small stones. Traps were placed at only 9 representative sites with 8 traps at each, randomly distributed, during the spring of 1982.

In all cases, the material was collected in person by C. URONES, thus avoiding the disparities due to the capturing by different investigators (CANARD, 1981).

The collection methods employed do serve to establish a comparative number between each site although they do not yield density measurements. The results obtained with the different methods employed are not comparable though overall they complement each other and do provide information concerning the species present at each site. We are aware that the image of taxocenosis that is achieved with these data involves a certain deformation of the true reality of the situation and caution should thus be taken in the interpretation of the results (TURNBULL, 1973; CANARD, 1984).

2. Transport and conservation

The specimens captured were taken live to the laboratory and placed in separate glass tubes. The juveniles and subadults were fed weekly with *Drosophila melanogaster* until they reached maturity. After observing diverse aspects of the biology, copulatory and preying habits, etc., the spiders were conserved according to the traditional method in ethyl alcohol (70°) with glycerine.

3. Identification of the spiders

All the material collected was subjected to an exhaustive taxonomic study which made a broad bibliographic task necessary. The lack of a general work on the identification of Iberian species made it necessary to refer to certain non-Spanish works, with the omission of study of the endemic species that it involves. Basically, the works used are: SIMON, 1875, 1878, 1932; LOCKET & MILLIDGE, 1951; LOCKET & al., 1974; REIMOSER, 1937; TULLGREN, 1944, 1946; DONDALE & REDNER, 1978, 1982, and different catalogues (BONNET, 1945-1961; BRIGNOLI, 1983; FERNANDEZ GALIANO, 1910; PEREZ DE ROMAN, 1957), and numerous articles published in diverse journals such as: Ann. Soc. ent. France, An. Soc. esp. Hist. nat.; Boletín Asoc. esp. Entom.; Bull. British Arachnol. Soc.; Bull. Soc. Hist. nat. Toulouse; Mem. Est. Mus. Zool. Univ.

n°	Fr	$\hat{H}(E)$	n°	Fr	$\hat{H}(E)$
Fam. Anyphaenidae					
1. <i>Anyphaena accentuata</i> (Walck., 1802)	7	0.36	42. <i>P. emarginatus</i> (Schränk, 1803)	6	0.33
2. <i>A. albirrorata</i> Simon, 1878	3	0.22	43. <i>P. histrio</i> (Latreille, 1819)	1	0.07
3. <i>A. numida</i> Simon, 1897	19	0.70	44. <i>P. margaritatus</i> (Clerck, 1758)	1	0.13
4. <i>A. sabina</i> L. Koch, 1866	4	0.26	45. <i>P. pulchellus</i> Lucas, 1846	12	0.51
Fam. Clubionidae					
5. <i>Agroeca inopina</i> O. P.-Cambr., 1866	3	0.17	46. <i>P. ruficapillus</i> Simon, 1875	13	0.56
6. <i>Castianeira badia</i> (Simon, 1877)	2	0.13	47. <i>P. rufus</i> Walckenaer, 1826	19	0.70
7. <i>Chiracanthium elegans</i> Thorell, 1875	3	0.17	48. <i>Thanatus formicinus</i> (Clerck, 1758)	1	0.07
8. <i>C. erraticum</i> (Walckenaer, 1802)	1	0.07	49. <i>T. lineatipes</i> Simon, 1870	6	0.33
9. <i>C. pelasgicum</i> (C.L. Koch, 1837)	11	0.51	50. <i>T. oblongiusculus</i> (Lucas, 1846)	26	0.82
10. <i>C. pennatum</i> Simon, 1878	2	0.13	51. <i>T. striatus</i> C.L. Koch, 1845	3	0.17
11. <i>C. pennyi</i> O. P.-Cambridge, 1873	4	0.26	52. <i>T. vulgaris</i> Simon, 1870	22	0.77
12. <i>C. punctatorum</i> (Villers, 1789)	16	0.64	53. <i>Tibellus macellus</i> Simon, 1875	2	0.13
13. <i>C. seidlitzii</i> L. Koch, 1864	5	0.29	54. <i>T. oblongus</i> (Walckenaer, 1802)	9	0.42
14. <i>C. striolatum</i> Simon, 1878	21	0.74	Fam. Thomisidae		
15. <i>Clubiona aducta</i> Simon, 1932	2	0.13	55. <i>Diaea dorsata</i> (Fabricius, 1777)	1	0.07
16. <i>C. brevipes</i> Blackwall, 1841	1	0.07	56. <i>Heriaeus mellottei</i> Simon, 1886	15	0.60
17. <i>C. compta</i> C.L. Koch, 1839	3	0.22	57. <i>Misumena vatia</i> (Clerck, 1758)	37	0.95
18. <i>C. corticalis</i> (Walckenaer, 1802)	2	0.13	58. <i>Misumenops tricuspidatus</i> (Fabricius, 1775)	7	0.33
19. <i>C. genevensis</i> L. Koch, 1866	3	0.17	59. <i>Monaeses paradoxus</i> (Lucas, 1846)	1	0.07
20. <i>C. neglecta</i> O. P.-Cambridge, 1862	5	0.26	60. <i>Oxyptila bicuspid</i> Simon, 1932	3	0.17
21. <i>C. terrestris</i> Westring, 1851	1	0.07	61. <i>O. blitea</i> Simon, 1875	3	0.17
22. <i>C. vegeta</i> L. Koch, 1874	2	0.13	62. <i>O. pauxilla</i> (Simon, 1870)	2	0.13
23. <i>Liocranum majus</i> Simon, 1878	17	0.66	63. <i>O. simplex</i> (O. P.-Cambridge, 1862)	3	0.17
24. <i>Mesiotelus mauritanicus</i> Simon, 1909	2	0.13	64. <i>O. umbraculorum</i> Simon, 1932	1	0.07
25. <i>Micaria albimana</i> O. P.-Cambridge, 1872	5	0.29	65. <i>Pistius truncatus</i> (Pallas, 1772)	12	0.53
26. <i>M. guttigera</i> Simon, 1878	3	0.22	66. <i>Runcinia lateralis</i> (C.L. Koch, 1838)	59	0.97
27. <i>M. romana</i> L. Koch, 1866	1	0.07	67. <i>Synaena globosum</i> (Fabricius, 1775)	74	0.82
28. <i>M. triguttata</i> Simon, 1884	1	0.07	68. <i>Thomisus onustus</i> Walckenaer, 1805	83	0.66
29. <i>Phrurolithus festivus</i> (C.L. Koch, 1835)	3	0.22	69. <i>Tmarus piger</i> (Walckenaer, 1802)	1	0.07
30. <i>P. nigrinus</i> (Simon, 1878)	1	0.07	70. <i>T. staintoni</i> (O. P.-Cambridge, 1873)	3	0.17
31. <i>Scotina celans</i> (Blackwall, 1841)	3	0.22	71. <i>Xysticus acerbus</i> Thorell, 1872	29	0.87
32. <i>S. palliardi</i> (L. Koch, 1881)	1	0.07	72. <i>X. audax</i> (Schränk, 1803)	4	0.26
Fam. Sparassidae					
33. <i>Eusparassus dufourii</i> Simon 1932	27	0.84	73. <i>X. bufo</i> (Dufour, 1820)	5	0.29
34. <i>Micrommata ligurinum</i> (C.L. Koch, 1845)	33	0.91	74. <i>X. caperatus</i> Simon, 1875	1	0.07
35. <i>Olios argelasius</i> (Walckenaer, 1806)	5	0.26	75. <i>X. cor</i> Canestrini, 1873	3	0.17
Fam. Zoridae					
36. <i>Zora manicata</i> Simon, 1878	3	0.17	76. <i>X. cristatus</i> (Clerck, 1758)	1	0.07
37. <i>Z. spinimana</i> (Sundevall, 1832)	3	0.17	77. <i>X. erraticus</i> (Blackwall, 1834)	14	0.58
Fam. Philodromidae					
38. <i>Philodromus aureolus</i> (Clerck, 1758)	1	0.07	78. <i>X. ferrugineus</i> Menge, 1876	21	0.74
39. <i>P. buxi</i> Simon, 1884	3	0.17	79. <i>X. gallicus</i> Simon, 1875	3	0.17
40. <i>P. cespitum</i> (Walckenaer, 1802)	64	0.94	80. <i>X. grillator</i> Simon, 1932	4	0.26
41. <i>P. dispar</i> Walckenaer, 1826	22	0.77	81. <i>X. ibex</i> Simon, 1875	8	0.39
			82. <i>X. kempelini</i> Thorell, 1872	11	0.51
			83. <i>X. kochi</i> Thorell, 1872	19	0.70
			84. <i>X. lanio</i> C.L. Koch, 1835	8	0.39
			85. <i>X. ninnii</i> Thorell, 1872	19	0.70
			86. <i>X. nubilus</i> Simon, 1875	26	0.82
			87. <i>X. robustus</i> (Hahn, 1831)	2	0.13
			88. <i>X. sabulosus</i> (Hahn, 1831)	8	0.39
			89. <i>X. semicarinatus</i> Simon, 1932	20	0.72
			90. <i>X. striatipes</i> L. Koch, 1870	6	0.33

Table I. — List of species collected. For each species, a reference number (n°), its relative frequency (Fr) and entropy ($\hat{H}(E)$) are given.

Coimbra; Mis. Zool.; Proc. Zool. Soc. London,... among others. We also consulted the material at the Museo Español de Ciencias Naturales in Madrid and the Museum national d'Histoire naturelle in Paris.

All these sources permitted a satisfactory classification of the spiders captured.

Superfamilies	Families	Genera	Species	
Clubionoidea	Anyphaenidae	1	4	37
	Clubionidae	9	28	
	Sparassidae	3	3	
	Zoridae	1	2	
Thomisoidea	Philodromidae	3	17	53
	Thomisidae	12	36	
2	6	29	90	

Table II. — List of number of species and genera grouped by families and superfamilies.

Results and discussion

1. List of species

The overall species inventory (table I) comprising 90 species (37 species of Clubionoidea and 53 of Thomisoidea) grouped in 29 genera and 6 families (table II) was established.

It may be seen that the Thomisidae, Clubionidae and Philodromidae, in this order, are the major families with respect to the number of species. Among the genera, the best represented regarding their richness of species are: *Xysticus* (20), *Philodromus* (10), *Chiracanthium* (8), *Clubiona* (8), *Oxyptila* (5), and *Thanatus* (5).

Regarding the proportion between the genera and species captured in terms of the literature cited for the Iberian Peninsula and Balearic Islands, the percentages were as follows:

Families	genera	species
Anyphaenidae	100 %	100 %
Clubionidae	75 %	50 %
Sparassidae	100 %	75 %
Zoridae	100 %	33.33 %
Philodromidae	100 %	45.95 %
Thomisidae	85.71 %	58.06 %

In all of the families 75 % of the genera cited for the Iberian Peninsula and Balearic Islands are surpassed (or at least equalled) and only in two cases are values lower than 50 % for the species recorded, which shows that the zone has a very rich and diverse fauna. This richness is due to the peculiar characteristics of the zones chosen, which have already been commented on in the section on the environment.

2. Analysis of species distribution

Calculation of the relative frequencies (GODRON, 1968) (table I) provided knowledge of the most representative species in the general composition of the fauna of the area studied, after having distributed the values of the 6 classes according to the percentage of presence (table III). Upon examining this distribution, it is seen that of the 90 species present in the zone, 26 are present at less than 10 % of sampling sites (classes 1 and 2), in contrast with the small number of species that are very common: only 1, fairly common: 3 and common: 6.

Class 6 very common (100-75 %)	<i>T. onustus</i>			1 sp.
Class 5 fairly common (75-50 %)	<i>P. cespitum</i> <i>R. lateralis</i> <i>S. globosum</i>			3 sp.
Class 4 common (50-25 %)	<i>E. dufouri</i> <i>M. ligurinum</i> <i>T. oblongiusculus</i>	<i>M. vatia</i> <i>X. acerbus</i> <i>X. nubilus</i>		6 sp.
Class 3 rather uncommon (25-10 %)	<i>A. numida</i> <i>C. pelagicum</i> <i>C. punctorium</i> <i>C. striolatum</i> <i>L. majus</i> <i>P. dispar</i>	<i>P. pulchellus</i> <i>P. ruficapillus</i> <i>P. rufus</i> <i>T. vulgaris</i> <i>H. mellottei</i> <i>P. truncatus</i>	<i>X. erraticus</i> <i>X. ferrugineus</i> <i>X. kempelini</i> <i>X. kochi</i> <i>X. ninnii</i> <i>X. semicarinatus</i>	18 sp.
Class 2 rare uncommon (10-2 %)	<i>A. accentuata</i> <i>A. albirrorata</i> <i>A. sabina</i> <i>A. inopina</i> <i>C. elegans</i> <i>C. pennyi</i> <i>C. seidlitzi</i> <i>C. compta</i> <i>C. genevensis</i> <i>C. neglecta</i> <i>M. albimana</i> <i>M. guttigera</i>	<i>P. festivus</i> <i>S. celans</i> <i>O. argelasius</i> <i>Z. manicata</i> <i>Z. spinimana</i> <i>P. buxi</i> <i>P. emarginatus</i> <i>T. lineatipes</i> <i>T. striatus</i> <i>T. oblongus</i> <i>M. tricuspidata</i> <i>O. bicuspis</i>	<i>O. blitea</i> <i>O. simplex</i> <i>T. staintoni</i> <i>X. audax</i> <i>X. bufo</i> <i>X. cor</i> <i>X. gallicus</i> <i>X. grillator</i> <i>X. ibex</i> <i>X. lanio</i> <i>X. sabulosus</i> <i>X. striatipes</i>	36 sp.
Class 1 very rare (2 %)	<i>C. badia</i> <i>C. erraticum</i> <i>C. pennatum</i> <i>C. aducta</i> <i>C. brevipes</i> <i>C. corticalis</i> <i>C. terrestris</i> <i>C. vegeta</i> <i>M. mauritanicus</i>	<i>M. romana</i> <i>M. triguttata</i> <i>P. nigrinus</i> <i>S. palliardii</i> <i>P. aureolus</i> <i>P. histrio</i> <i>P. margaritatus</i> <i>T. formicinus</i> <i>T. macellus</i>	<i>O. dorsata</i> <i>M. paradoxus</i> <i>O. pauxilla</i> <i>O. umbraculorum</i> <i>T. piger</i> <i>X. caperatus</i> <i>X. cristatus</i> <i>X. robustus</i>	26 sp.

Table III. — Distribution of species in classes according to their relative frequencies.

Overall, the community of Clubionoidea and Thomisoidea spiders from the region studied may said to be balanced (LUCZAK, 1960) and fairly diversified.

One concept of great importance when searching for the relationship between species and environmental factors is *entropy-species* ($\hat{H}(E)$), which is calculated from the number of presences and absences of each species in the total set of sampling (GODRON, 1968).

The highest entropy values are shown by the species with a relative frequency close to 50 % (e.g. *Runcinia lateralis*, $\hat{H}(E) = 0.97$). By contrast, the species present (or absent) in the majority of the sampling exhibit an entropy-species close to zero. Accordingly, when drawing conclusions about the ecological relationships between species and environmental factors we used only those entropy-species was greater than 0.150 bits and discarded the 26 species appearing sporadically.

3. Seasonal evolution of the adults of different species

The captures, spread evenly over time, point to the existence of seasonal fluctuations in the spider populations. We grouped the species whose suitable field and laboratory data were available to us, with reference to the time of the year during which their adults are predominant or exclusive. This was independent of the duration of their life cycles, which was dealt with elsewhere (URONES, 1985, 1986, in press; URONES & GOMEZ, in press).

These groups were as follows:

1. Spring species. Among these we distinguish those appearing at the following times:

a. At the end of winter and during spring: *Chiracanthium striolatum*, *Micrommata ligurinum*, *Philodromus emarginatus*, *P. ruficapillus*, *P. rufus* and *Thanatus lineatipes*.

b. Only in spring: *Clubiona aducta*, *C. corticalis*, *Micaria guttigera*, *Eusparassus dufouri* and *Zora manicata*.

c. During spring and at the beginning of summer: *Chiracanthium seidlitzi*, *Philodromus pulchellus*, *Tibellus oblongus*, *Heriaeus mellottei*, *Xysticus ibex* and *X. semicarinatus*.

2. Summer species. Among these two subgroups can be distinguished:

a. Species appearing towards the end of spring and in summer: *Clubiona neglecta*, *Thanatus oblongiusculus*, *T. vulgaris*, *Runcinia lateralis* and *Xysticus erraticus*.

b. Summer species: *Chiracanthium pennyi*, *C. punctorium*, *Micaria albimana*, *Zora spinimana* and *Xysticus ninnii*.

3. Autumn species. These are found from the end of summer and in autumn: *Oxyptila blitea*, *Xysticus grallator* and *X. striatipes*.

4. Species of greater amplitude:

a. In winter and spring: *Anyphaena accentuata*, *A. numida*, *Agroeca inopina*, *Chiracanthium pelasgicum*, *Scotina celans*, *Philodromus dispar*, *Xysticus lanio*, *X. acerbus* and *X. kempelini*.

b. In winter, spring and the beginning of summer: *Xysticus nubilus*.

c. At the end of winter, in spring and summer: *Misumena vatia*, *Synaema globosum* and *Xysticus kocki*.

d. In spring and summer: *Philodromus cespitum*.

e. At the end of summer, in autumn and in winter: *Xysticus sabulosus*.

f. In autumn, winter and the beginning of spring: *Anyphaena alboirrorata* and *Liocranum majus*.

It may be seen that throughout the territory studied, spring is the most propitious season for the capture of adults belonging to the greatest number of species within the taxocenosis considered.

Conclusions

With the use of several different and complementary methods of capture, the results show that the community of Clubionoidea and Thomisoidea spiders is balanced and fairly diversified. The great richness in spiders is possibly due to the peculiar

characteristics of the Central System, with large differences in altitude and a pronounced Atlantic influence from the west, both of which contribute to great diversity in the prevailing ecological conditions.

In the zone studied, spring is the season in which active adults belonging to the greatest number of species are found.

We feel that it would have been of great interest to complement this study and compare it with others carried out in different parts of the Iberian Peninsula; this unfortunately has not been possible because such studies do not exist.

II. MUTUAL INFORMATION

Introduction

One topic of paramount interest in ecology is to discover the mutual relationships existing between species and environmental factors since it is accepted by all researchers that living organisms, and especially animals, are able to detect, select or actively seek out the environments most suitable for them within the environmental mosaic, thus establishing a correspondance between the properties of the environment and the characteristics of the species (MARGALEF, 1982).

The methods employed for the analysis of such relationships may be divided into two main groups: analytical methods, that study the relationships between each species and a variable (or group of variables), and multidimensional methods that allow one to study the relationships of the set of species with the set of variables.

The aim of the present part is to use a mathematical analytical method (mutual information) to attempt to establish the role of certain environmental factors in the distribution of spider species. The multidimensional study will be dealt with in the last part.

Methods

Regarding the mathematical analytical method of mutual information, this was based on the concept of *ecological factor*, understanding by this «any character of the physical or biotic surroundings able to act on the distribution of species in nature» (GOUNOT, 1969).

The influence of any ecological factor (or environmental variable) can be evaluated as long as that factor shows a certain degree of variability. According to this, the factor is divided into a certain number of classes from which the ecological profile of a single species for a single factor is constructed (DAGET & GODRON, 1982).

The information provided by an ecological profile may be evaluated by means of the entropy-factor which allows one to discover which are the indicative species with respect to a given factor and which are the active factors; i.e., those that play the most relevant role in the distribution of the species.

All these concepts have arisen and have been developed from phytoecological studies (GODRON, 1968; GOUNOT, 1969; DAGET & GODRON, 1982) and have thus been used in numerous studies on vegetation and occasionally in zoecology (BLONDEL, 1979), although their use is novel in the case of spider ecology.

Results and discussion

As was pointed out in the previous part, a total of 90 species of Clubionoidea and Thomisoidea were collected and although the relationship of all of them with the different environmental factors was analyzed, for representing and obtaining the conclusions only those entropy-species was greater than 0.150 bits were used, and the 26 sporadic species were discarded (table I).

To make the results of the captures made at the 118 sites homogeneous, we considered for each species the maximum number of species captured per unit of effort made (half an hour sampling) on the different visits.

Three macroscopic variables were analyzed: altitude, vegetation and continentality, because they are the easiest to measure, observe and quantify. In fact, these are a reflection of other ecological factors and one may therefore expect them to have a clearer relationship with the distribution of species than would be likely with individual ecological factors such as temperature, rainfall, sunshine, etc.

1. Altitude

This factor was divided into 9 classes: 8 of 200 m of amplitude, from 200 m a.s.l. to 1800 m a.s.l.; above this height, only one class was considered owing to the great homogeneity of such high areas and their faunistic poverty.

The entropy-factor obtained using the GODRON's (1968) formula is 2.87 bits, the maximum entropy-factor being of 3.18 bits. Accordingly, the quality of sampling has a value of 0.90, close to unity, and serves to conclude that the altitude variable has been well-sampled.

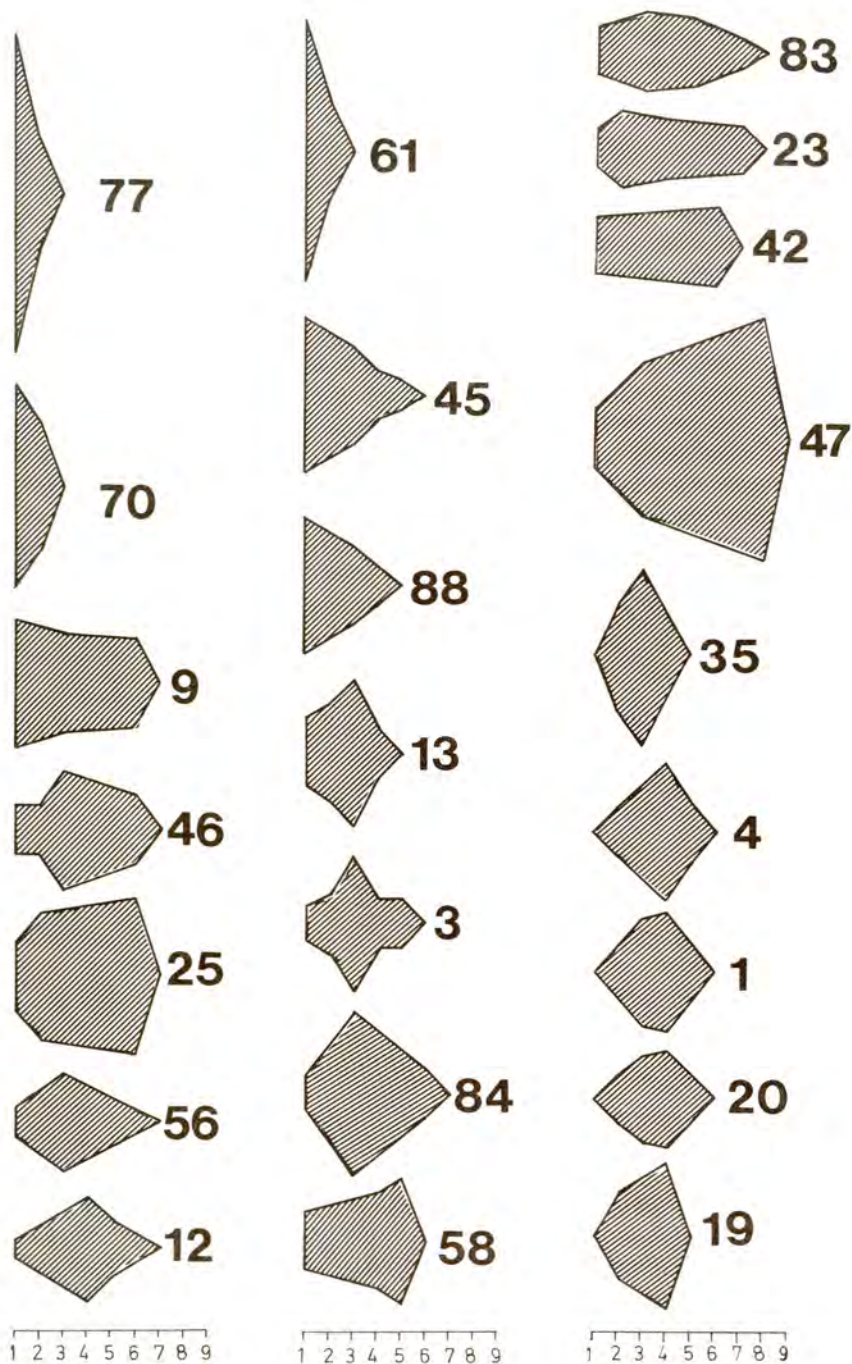
Following the indications of DAGET & GODRON (1982), we plotted graphically the frequency profiles corrected by grouping the species with similar ecological profiles (fig. 2). These profiles permit one to see the amplitude of tolerance of each species with respect to the altitude factor and the preferences of the species regarding the different states of the factor.

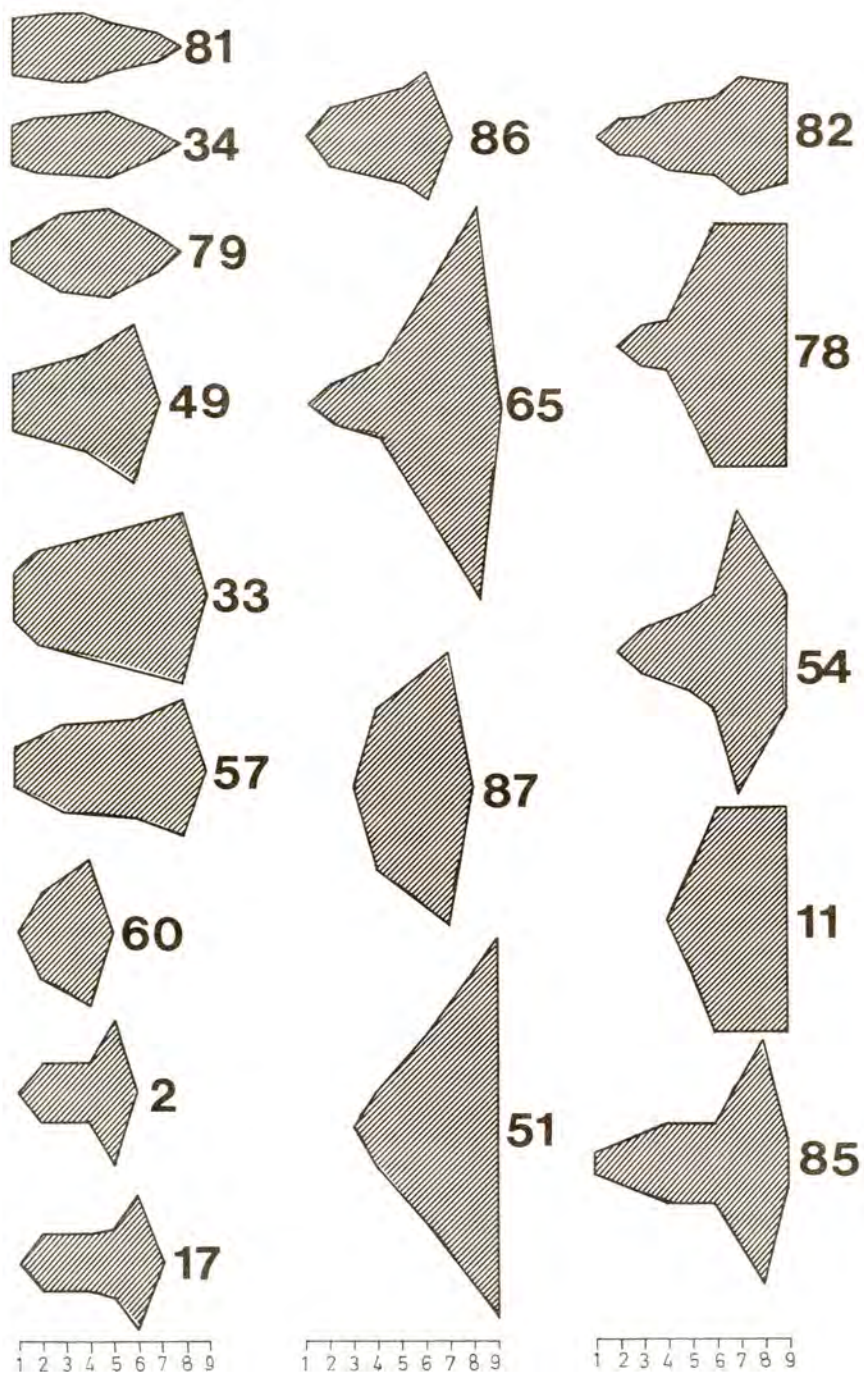
From the joint study of these ecological profiles and from the indicative value of each species for the altitude factor (on the basis of the mutual information shown in table IV), it is possible to establish groups of species with similar behaviour with respect to the altitude factor as follows:

a. There are species that preferentially inhabit the low altitude zone, either restricted to that zone, such as *Xysticus grallator* (between 200-600 m) or with greater amplitude, such as *Philodromus pulchellus*, *Chiracanthium pelasgicum*, *Runcinia lateralis*, and *Synaema globosum*.

b. There are species which are most frequent in the intermediate altitude classes (600-1200 m) although they exhibit a different ecological amplitude for the variable. Among these, noteworthy are *Anyphaena accentuata*, *Philodromus dispar*, *Xysticus lanio*, *Micaria albimana*, *Anyphaena numida*, *Xysticus kempelini*, and *Heriaeus melottei*.

c. Other species show a marked preference for the high zones: *Chiracanthium pennyi*, *Xysticus ibex*, *X. semicarinatus*, and *X. striatipes*.





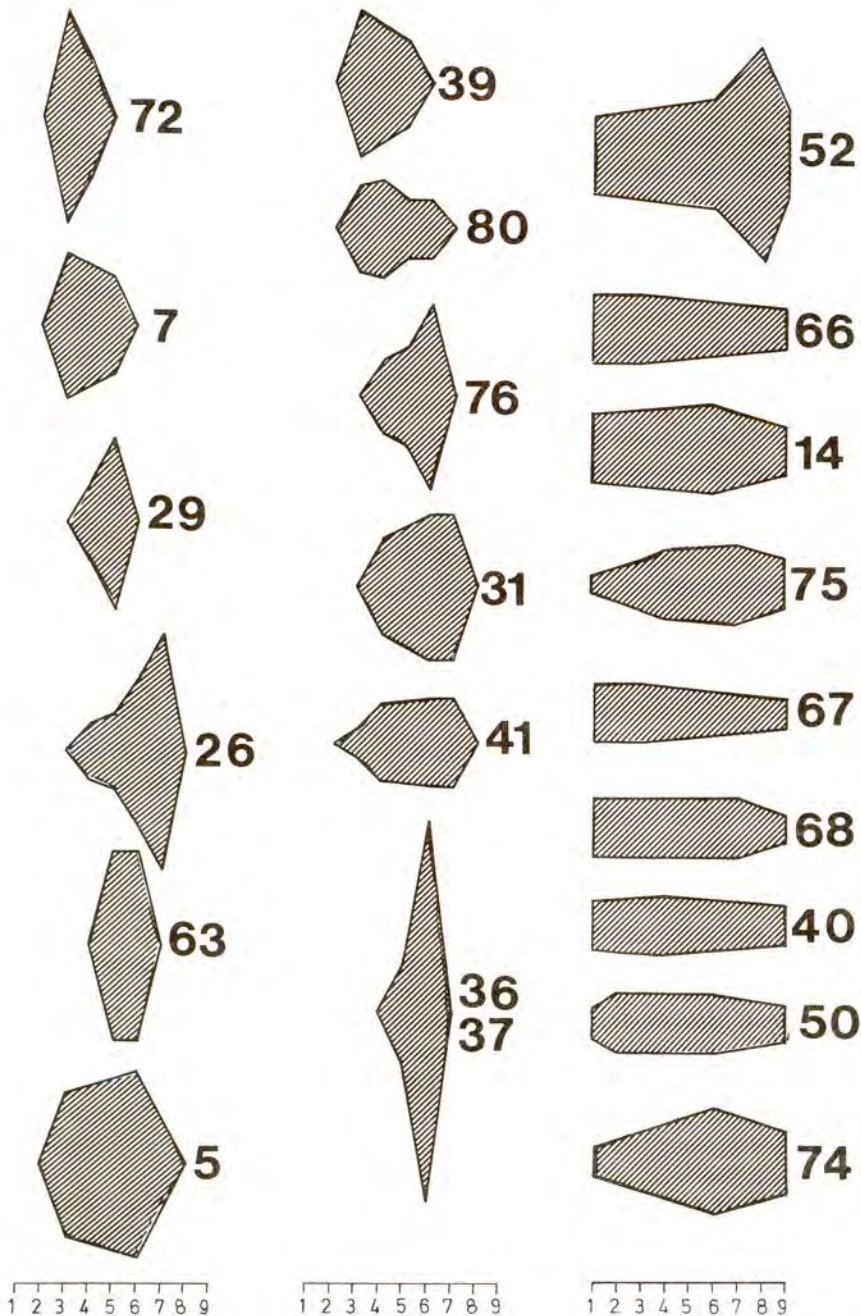


Figure 2. — Representation of corrected frequency profiles for the altitude factor (1 = 200-400 m a.s.l., 2 = 400-600 m, 3 = 600-800 m, 4 = 800-1000 m, 5 = 1000-1200 m, 6 = 1200-1400 m, 7 = 1400-1600 m, 8 = 1600-1800 m, 9 = 1800-2400 m). The numbers correspond to the species show in table I.

n°	Species	I(L;E)	n°	Species	I(L;E)
81	<i>X. ibex</i> Simon	0.25	68	<i>T. onustus</i> Walckenaer	0.05
47	<i>P. rufus</i> Walckenaer	0.17	88	<i>X. sabulosus</i> (Hahn)	0.05
54	<i>T. oblongus</i> (Walckenaer)	0.13	4	<i>A. sabina</i> L. Koch	0.04
90	<i>X. striatipes</i> L. Koch	0.13	5	<i>A. inopina</i> O. P.-Cambridge	0.04
41	<i>P. dispar</i> Walckenaer	0.12	10	<i>C. pennatum</i> Simon	0.04
57	<i>M. vatia</i> (Clerck)	0.11	13	<i>C. seidlitzi</i> L. Koch	0.04
66	<i>R. lateralis</i> (C.L. Koch)	0.11	18	<i>C. corticalis</i> (Walckenaer)	0.04
67	<i>S. globosum</i> (Fabricius)	0.11	19	<i>C. genevensis</i> L. Koch	0.04
85	<i>X. ninnii</i> Thorell	0.11	20	<i>C. neglecta</i> O. P.-Cambridge	0.04
3	<i>A. numida</i> Simon	0.10	22	<i>C. vegeta</i> L. Koch	0.04
33	<i>E. dufouri</i> Simon	0.10	26	<i>M. guttigera</i> Simon	0.04
80	<i>X. grallator</i> Simon	0.10	29	<i>P. festivus</i> (C.L. Koch)	0.04
25	<i>M. albimana</i> O. P.-Cambridge	0.09	40	<i>P. cespitum</i> (Walckenaer)	0.04
45	<i>P. pulchellus</i> Lucas	0.09	60	<i>O. bicuspsis</i> Simon	0.04
52	<i>T. vulgaris</i> Simon	0.09	70	<i>T. staintoni</i> (O. P.-Cambridge)	0.04
11	<i>C. pennyi</i> O. P.-Cambridge	0.08	73	<i>X. bufo</i> (Dufour)	0.04
12	<i>C. punctorium</i> (Villers)	0.08	2	<i>A. albirrorata</i> Simon	0.03
53	<i>T. macellus</i> Simon	0.08	6	<i>C. badia</i> (Simon)	0.03
58	<i>M. tricuspidatus</i> (Fabricius)	0.08	7	<i>C. elegans</i> Thorell	0.03
62	<i>O. pauxilla</i> (Simon)	0.08	23	<i>L. majus</i> Simon	0.03
65	<i>P. truncatus</i> (Pallas)	0.08	27	<i>M. romana</i> L. Koch	0.03
89	<i>X. semicarinatus</i> Simon	0.08	28	<i>M. triguttata</i> Simon	0.03
9	<i>C. pelasgicum</i> (C.L. Koch)	0.07	30	<i>P. nigrinus</i> (Simon)	0.03
14	<i>C. striolatum</i> Simon	0.07	38	<i>P. aureolus</i> (Clerck)	0.03
34	<i>M. ligurinum</i> (C.L. Koch)	0.07	43	<i>P. buxi</i> Simon	0.03
82	<i>X. kemplelini</i> Thorell	0.07	59	<i>M. paradoxus</i> (Lucas)	0.03
83	<i>X. kochi</i> Thorell	0.07	69	<i>T. piger</i> (Walckenaer)	0.03
84	<i>X. lanio</i> C.L. Koch	0.07	75	<i>X. cor</i> Canestrini	0.03
1	<i>A. accentuata</i> (Walckenaer)	0.06	79	<i>X. gallicus</i> Simon	0.03
36	<i>Z. manicata</i> Simon	0.06	8	<i>C. erraticum</i> (Walckenaer)	0.02
37	<i>Z. spinimana</i> (Sundevall)	0.06	15	<i>C. aducta</i> Simon	0.02
49	<i>T. lineatipes</i> Simon	0.06	16	<i>C. brevipes</i> Blackwall	0.02
56	<i>H. mellotiei</i> Simon	0.06	17	<i>C. compta</i> C.L. Koch	0.02
71	<i>X. acerbus</i> Thorell	0.06	21	<i>C. terrestris</i> Westring	0.02
72	<i>X. audax</i> (Schränk)	0.06	24	<i>M. mauritanicus</i> Simon	0.02
77	<i>X. erraticus</i> (Blackwall)	0.06	32	<i>S. palliardii</i> (L. Koch)	0.02
78	<i>X. ferrugineus</i> Menge	0.06	43	<i>P. histrio</i> (Latreille)	0.02
86	<i>X. nubilus</i> Simon	0.06	44	<i>P. margaritatus</i> (Clerck)	0.02
87	<i>X. robustus</i> (Hahn)	0.06	48	<i>T. formicinus</i> (Clerck)	0.02
31	<i>S. celans</i> (Blackwall)	0.05	50	<i>T. oblongiusculus</i> (Lucas)	0.02
35	<i>O. argelasius</i> (Walckenaer)	0.05	55	<i>D. dorsata</i> (Fabricius)	0.02
46	<i>P. ruficapillus</i> Simon	0.05	64	<i>O. umbraculorum</i> Simon	0.02
51	<i>T. striatus</i> C.L. Koch	0.05	74	<i>X. caperatus</i> Simon	0.02
61	<i>O. blitea</i> Simon	0.05	76	<i>X. cristatus</i> (Clerck)	0.02
63	<i>O. simplex</i> (O. P.-Cambridge)	0.05	42	<i>P. emarginatus</i> (Schränk)	0.01

Table IV. — Mutual information (in decreasing order) for each species with respect to altitude.

2. Vegetation

According to their structure, we distinguished 14 classes of vegetation, most of them including communities of the same phytosociological class represented by one or several alliances, except in the case of the class *Querceto-Fagetea*, where two alliances *Quercion robori-pyrenaica* and *Osmundo-Alnion* were considered independently, as were the disclimax forests of *Castanea sativa*; on the other hand, the pine copses were considered as a separate entity owing to their physiognomic homogeneity despite the fact that they were man-planted in areas that were originally quite different.

The cataloging was supervised by Prof. Dr. E. RICO (Department of Botany).

As in the previous case, we calculated the entropy-factor value; this proved to be of 3.46 bits, thus pointing to a high quality (0.91). The joint study of the corrected frequency profiles and the mutual information for each species with respect to this factor allowed us to establish a direct relationship between the type of vegetation and some of the species.

Accordingly a series of species is associated to the deciduous forests of *Querceto-Fagetea*, either to the three kinds of forests (oak groves, chestnut groves and alders) present in the zone, such as *Philodromus buxi*, or two of them (6 species: *Agroeca inopina*, *Scotina celans*, *Zora manicata*, *Z. spinimana*, *Xysticus gallicus* and *Chiracanthium elegans*). *Philodromus dispar* also lives in these forests and has extended to the pine copses planted in oak climax.

Five species (*Anyphaena accentuata*, *Clubiona neglecta*, *Xysticus erraticus*, *X. lanio*, and *Chiracanthium seidlitzi*), apart from these woods, also occupy the grasslands of *Arrhenatheretea* in the clearings and 2 species are restricted exclusively to these grasslands: *Thanatus striatus* and *Oxyptila simplex*.

Present throughout almost all the vegetation formations related to the oak and extending to the mountain grasslands are: *Xysticus ferrugineus*, *X. ibex* and *X. semicarinatus*.

Chiracanthium pennyi and *Tibellus oblongus* are found exclusively on sites with damp or waterlogged soils, either grasslands or peat bogs.

Towards the end of summer and during autumn, one finds *Xysticus grallator* on markedly nitrophile zones that are waterlogged during the spring.

Clubiona compta appears in all the forests of the zone regardless of the type. By contrast, *Chiracanthium punctorium* shows a preference for open zones without a tree covering.

Some species are present in the majority of the classes and even *Philodromus cespitum*, *Runcinia lateralis*, *Synaema globosum* and *Thomisus onustus* are found, with different abundances, in all the classes of vegetation considered.

The species that appear exclusively in one class of vegetation cannot be considered as representative with the exception of *Diaea dorsata* found only in the mixed forest of La Honfria (Linares de Riofrio in the province of Salamanca) and this possibly reflects the special vegetation in this enclave, with numerous species characteristic of beech groves and other deciduous forests of Eurosiberian region.

3. Oceanic influence (continentality)

Since among the various factors that determine the continentality of a site the distance from the ocean is the easiest to measure and hence the safest parameter, and

because the large extension of the study zone suggests the existence of strong differences in the degree of continentality simply as a reflection of such distances, the zone was divided into 8 classes, using the vertical lines of the U.T.M. coordinates separated in 20 km to establish the species that characterize the different areas of continental or oceanic influence in the central western part of the Central System.

The entropy-factor has a value of 2.82 bits and the quality of sample is very high (0.94).

The study of the ecological profiles and the mutual species-factor information allows one to establish the groups of species with similar behaviour with respect to this biogeographic variable.

a. One group of species appears preferentially in the locations closest to the ocean; among them, noteworthy are: *Anyphaena albirrorata*, *A. accentuata*, *Pistius truncatus*, *Olios argelasius* and *Thanatus lineatipes*.

b. Others are found on more continental zones: *Chiracanthium pennyi*, *C. seidlitzii*, *Tibellus oblongus*, *Xysticus sabulosus* and *X. semicarinatus*.

c. Some species appear in intermediate locations with no pronounced atlantic or continental influence: *Scotina celans*, *Xysticus bufo*, *Agroeca inopina* and *Philodromus ruficapillus*, among others.

d. There is one species that appears in the Atlantic and most continental locations but is missing in the intermediate areas: *Xysticus striatipes*.

e. Finally, one group of species is unaffected by the factor: *Xysticus erraticus*, *Thomisus onustus* and *Philodromus cespitum*.

Oceanic influence on both slopes of the Sierra independently

With a view to avoiding the heterogeneity of the classes confected for the study of continentality, as a consequence of the influence of the mountain chain that crosses the zone, an independent study of both sides of the Sierra was made. From a comparison of the results, the following may be deduced:

a. The importance of the Central System as a geographic barrier to the distribution of species, since a number of them present on one side are missing from the other. In this sense, 24 species are present on the north side and absent from the southern one: *Agroeca inopina*, *Chiracanthium erraticum*, *C. pennyi*, *Clubiona brevipipes*, *C. corticalis*, *C. terrestris*, *Micaria guttigera*, *M. romana*, *M. triguttata*, *Phrurolithus festivus*, *P. nigrinus*, *Scotina celans*, *Zora manicata*, *Z. spinimana*, *Philodromus aureolus*, *P. histrio*, *Thanatus formicinus*, *T. striatus*, *Tibellus macellus*, *Diaea dorsata*, *Xysticus audax*, *X. cristatus*, *X. striatipes*, and *X. robustus*.

By contrast, 13 species are found on the southern side but are missing on the northern counterpart: *Castianeira badia*, *Clubiona vegeta*, *Mesiotelus mauritanicus*, *Scotina paillardii*, *Philodromus margaritatus*, *Monaeses paradoxus*, *Oxyptila blitea*, *O. pauxilla*, *O. umbraculorum*, *Tmarus staintoni*, *Xysticus grallator*, *X. bufo*, and *X. caperatus*.

In this sense, 77 species of Clubionoidea and Thomisoidea are present on the northern side and 66 on the southern side.

However, where the barrier of the Central System is less manifest, as in the case of the River Alagón basin, some species clearly from the southern side penetrate through such zones to fairly northern areas; this is the case of *Chiracanthium seidlitzii* and *Olios argelasius*.

b. Not only the presence or absence of species are indicative of the differences existing between the northern and southern sides; by comparing the percentages of presence of species common to both, differences are seen in the frequencies of such species between the two sides. In this sense the northern slope has more specimens of: *Philodromus dispar*, *Thanatus oblongiusculus*, *Xysticus nubilus*, and *X. semicarinatus*, among others. By contrast, the following are more common on the southern than on the northern side: *Eusparassus dufouri*, *Philodromus rufus*, *Anyphaena numida*, *Chiracanthium pelasgicum*, etc.

c. Upon comparing the corrected frequency profiles of the species obtained for the two sides of the mountain chain separately, some of them are seen to be in concordance with the fact that the southern side, with greater thermal attenuation and with a higher rainfall, is more oceanic than the northern side. One thus observes that:

— The more continental species of the southern side are found almost over the northern side, e.g., *Xysticus semicarinatus*, *Chiracanthium seidlitzi*, *Misumena vatia*, *Philodromus dispar*, and *Thanatus oblongiusculus*.

— The most continental species in the north slope do not appear in the south side: *Tibellus macellus*, *Chiracanthium pennyi*, *Clubiona corticalis*, *Agroeca inopina*, *Scotina celans*, *Xysticus robustus*, *Zora manicata*, and *Z. spinimana*.

— The more Atlantic species of the north are found throughout the southern part: *Chiracanthium pelasgicum*, *Xysticus nubilus*, *X. ferrugineus*, and *Philodromus cespitum*.

— The more Atlantic species from the south are not found in the north: *Xysticus grallator*, *Clubiona vegeta*, and *Olios argelasius*.

4. Influence of environmental factors

For each species separately

For each species separately, it is possible to establish the hierarchy of the activity of the ecological factors studied (altitude, vegetation, continentality, continentality on the northern side of the range and continentality on the southern slope). In this sense one observes a group of 14 species clearly influenced by the vegetation: *Xysticus semicarinatus*, *Thomisus onustus*, *Thanatus oblongiusculus*, *Runcinia lateralis*, *Philodromus rufus*, *Xysticus erraticus*, *Pistius truncatus*, *Heriaeus mellottei*, *Thanatus vulgaris*, *Xysticus acerbus*, *X. ninnii*, *X. lanio*, *Philodromus pulchellus*, and *Olios argelasius*.

There are two species that are clearly more influenced by the altitude factor (*Xysticus ibex* and *X. grallator*), although they are strongly affected by the vegetation.

Regarding the species in which continentality is the most determinant variable, two groups may be distinguished: one more influenced by the continentality of the southern side, formed by six species (*Micaria albimana*, *Liocranum majus*, *Anyphaena albirrorata*, *Synaema globosum*, *Xysticus sabulosus*, and *Chiracanthium seidlitzi*), and another six species that are affected by the continentality of the northern slope (*Xysticus nubilus*, *X. striatipes*, *Chiracanthium striolatum*, *Philodromus dispar*, *Scotina celans*, *X. kochi*, and *Anyphaena numida*).

Finally, some species appear that are influenced by more than one factor at the same time; this is the case of: *Chiracanthium punctarium*, *C. pelasgicum*, *C. pennyi*,

Anyphaena accentuata, *Eusparassus dufouri*, *Micrommata ligurinum*, *Misumena vatia*, *Philodromus cespitum*, *P. ruficapillus*, *Tibellus oblongus*, *Xysticus ferrugineus*, and *Oxyptila blitea*.

For a set of species

We also established the efficiency of the factors for a set of species, taking a group of indicative species and another of representative species (table V). One observes that vegetation is the most efficacious factor in the distribution of species, followed by continentality of the area and altitude. This finding of the greater importance of vegetation was logical and to be expected since the vegetation itself of a given site is a consequence of all the factors affecting the zone and is thus a reflection of their joint action. In most of the sites the greatest modifiers of the macroclimates are the plants. The class, density and structure of the covering of vegetation (rather than its composition) determine the microclimates that affect the spiders inhabiting them, as pointed out by LUCZAK (1963) in Poland.

The results of the present study are partially in agreement with those described by BLONDEL (1979) for the distribution of birds in Mont Ventoux (France); this author found vegetation and altitude among the most efficacious factors, whereas altitude was reported to provide little information; this must undoubtedly be due to the peculiar location of the French region studied and the zoological group considered.

Environmental factors	n° of classes	Entropy-factor		Sampling quality	Mutual information	Mutual information
		observed	maximum		mean value of 30 indicative species	mean value of 30 representative sp.
Altitude	9	2.87	3.18	0.90	0.09	0.08
Vegetation	14	3.46	3.82	0.91	0.17	0.16
Continentality	8	2.82	3.01	0.94	0.08	0.07
Continentality of N face	8	2.90	3.01	0.96	0.13	0.12
Continentality of S face	8	2.60	3.01	0.86	0.12	0.10

Table V. — Summary of the autoecological analysis with respect to the different environmental factors studied.

III. MULTIDIMENSIONAL ANALYSIS

Introduction

Few arachnologists have performed ecological studies in the Iberian Peninsula. In fact, it could be said that since the work by DIZ & OTERO (1978), the only works carried out have come from the Department of Ecology of the University of Salamanca (URONES, 1984; GALLARDO, 1985; CASTRILLO, 1986; FERNANDEZ-JOAQUIN, 1986). Although faunistic, taxonomic and morphological studies are more abundant, and sometimes include certain references to spider ecology (CAMARGO, 1982), it should be understood that Spanish research in this field is still in its infancy.

In word-wide terms, the reviews by TURNBULL (1973) and CHRISTOPHE & al. (1979), each focusing, respectively, on North America and Europe, together comprise more than 500 works on spiders ecology. However, on scarce occasions the arachnologists apply multivariant analysis methods, widely used for many years in other fields. As a final synthesis of parts I and II of this work, our aim here is to provide an overall view of the different spider communities with respect to their habitats and we have thus found it essential (or at least advisable) to resort to the use of such techniques.

Methods

The basic aspects regarding the territory, working protocol, sampling and species found can be seen in the first two parts of this work. Naturally, numerous methods can be used to show the dependence of species with respect to their environment (GOUNOT, 1969; MUELLER-DOMBOIS & ELLENBERG, 1974; WHITTAKER, 1974; etc.), and good proof of this is the autoecological treatment that has been performed. However, this kind of treatment, largely analytical, can be completed by providing a synthetic perspective, resorting, as will be detailed below, to multidimensional methods.

To determine relationships between species and site conditions, the importance value were transformed ($\log_{10}x + 1$), double standardized (BRAY & CURTIS, 1957) and ordinated using reciprocal averaging (RA; HILL, 1973, 1974). Because it does not assume monotonic linear responses of species along environmental gradients, this technique is preferable to most other ordination procedures, such as principal components analysis. GAUCH & al. (1981) have shown RA to be equally as effective as nonlinear multidimensional scaling (FASHAM, 1977; PRENTICE, 1977) but computationally more efficient. An additional advantage of RA technique is that it simultaneously creates an ordination of species and stands. By comparing axis scores for particular species, it is possible to identify diagnostic species or combinations of species for particular parts of the stand ordination. Analyses were performed by progressive fragmentation of the data; that is, after initial ordination, distinctive groups of stands, based on environmental conditions, were removed and the residual stands reordinated. In this way, the impact of the initially observed factor on subsequent analysis was greatly reduced. The specifics of this approach are described in PEET (1980).

Results and discussion

1. General analysis

Using all the data collected, a general ordering was made; this was an essential starting out point for later establishing precisions with the worst-defined groups or those of greatest interest. However, the great influence that sporadic species may exert on the resolution of the axes (GALINDO, 1985), together with the fact that a reasonable doubt always exists concerning the random nature of the sampling protocol leads to a situation whereby the elements (26 species) present at less than three sites have to be eliminated. We therefore started out from a set of data involving 118 sites $\times$ 64 species.

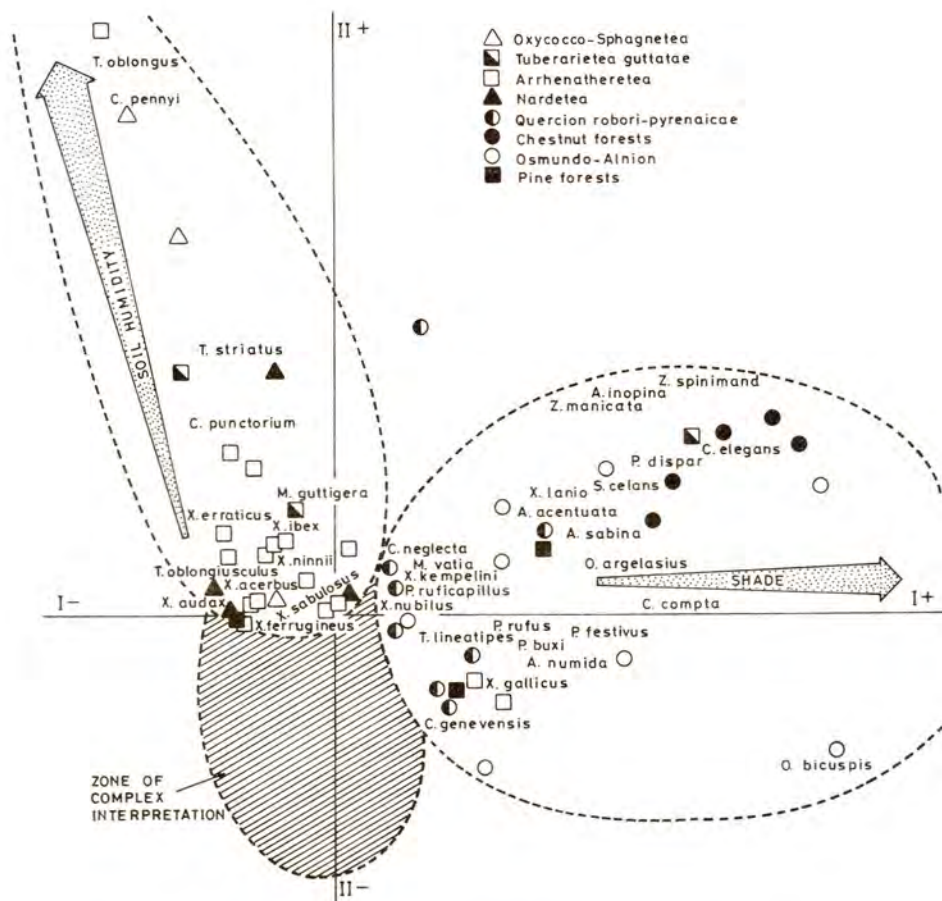


Figure 3. — Correspondence analysis with species present in at least 3 sites.

The percentages of inertia absorbed by the first two axes, respectively, are 7.6 and 6.6. The high environmental variability of the territory conditions such relatively low percentages; although speculations have been made concerning the ideal minima of absorption of inertia, and hence about the number of axes to be considered, in order to obtain a high degree of significance (see for example CUADRAS, 1981), the operative point in this kind of analysis is to achieve a situation whereby such minima are able to explain the presumably most influential environmental factors, and which is not detrimental to the reliability of the results (GIL, 1978).

Figure 3 shows the ordering of sites and species on the plane defined by the first two axes. From the negative values to the highest positive values axis I defines a shade gradient; around the origin and in the negative part of axis I are situated the low plant

formations, such as the different types of grasslands and moorland sampled (Cistaceae shrubs and heathlands). Around the positive part of axis I is grouped a set of sites with the common characteristic of having a high-altitude and closed-woodland vegetation, which affects the area by its shade and implies the predominance or exclusive presence of a set of species.

Within each group it may be seen that both the sites and the species are disposed according to the shade gradient referred to above. In this sense, oak forest (*Quercion robori-pyrenaicae*) and some grasslands (*Arrhenatheretea*) situated in their clearings predominate at the origin; associated to them are some species of spiders, among which the outstanding ones are *Clubiona neglecta*, *Misumena vatia*, *Xysticus kempeolini*, *X. nubilus*, and *Philodromus ruficapillus*. As higher values of axis I are reached, chestnut forests (*Castanea sativa*) begin to appear and gallery forests (*Osmundo-Alnion*); close to these is a series of species, some of which are *Chiracanthium elegans*, *Oxyptila bicuspis* and *Agroeca inopina*. It should be noted that within this group are included some sites belonging to other plant formations, as is the case of pine forests (*Pinus sylvestris*) repopulated in the oak (*Quercus pyrenaica*) domain.

Regarding the second axis, this clearly represents a soil humidity gradient, the sites which are flooded throughout almost the whole year (some grasslands and peat bogs of the class *Oxycocco-Sphagnetes*); close to this group are the species *Chiracanthium pennyi* and *Tibellus oblongus*. Following this, and with a lesser degree of soil humidity, are grouped the grasslands which can be included in the classes *Arrhenatheretea* and *Nardetea*; some plant formations of very similar soil humidity also appear, such as a grassland of *Agrostion castellanae* (class *Tuberarietea guttatae*) or a pine forest of *Pinus sylvestris*. Among the species closest to such sites are *Thanatus striatus*, *Chiracanthium puncturum*, *Xysticus erraticus*, *X. ibex*, *X. ninnii*, and *Micaria guttigera*.

Outstanding is the intermediate situation (outside the trace lines) of an oak forest at Candelario, which owing to its tree covering tends towards the shaded zones (positive part of axis I), although due to its high soil humidity would be included at the extreme positive end of axis II. The hatched area, which projects from the origin of the coordinates towards the negative part of axis II encompasses sites that are not very humid and that contain open vegetation. Since no trends of a clear-cut continuity can be seen, here we shall mention only that the extreme position is occupied by the sites on the southern slope of the Sierra, with the finding of *Xysticus grallator*, *Chiracanthium striolatum*, *Anyphaena albirrorata*, and *Eusparassus dufouri* close to them.

The relationship between the structure of the plant communities and the spider communities that inhabit them has been reported by different workers (LUCZAK, 1963; DUFFEY, 1966; TURNBULL, 1973; BULTMAN & al., 1982; CANARD, 1984). With the exception of certain spider linked to a particular type of plant, such as the case of certain Thomisidae species (SCHICK, 1965), it is evident that the characteristics of the plant covering will largely determine the appropriate habitat for the spiders and their prey, since the vegetation itself is a result of the compendium of the numerous environmental factors affecting it.

2. Analysis of the oak forests

The richness in vegetation of the oak forests (*Quercus pyrenaica* formations), which in fact constitute the climax of most of the sites studied, is related to the high

number of spider species and hence their particular treatment; with respect to epigeal coleopters, SAIZ & VASQUEZ (1980) also reported positive correlations between floristic and faunistic diversity. Once analyzed, the data table (16 sites $\times$ 64 species) yields absorptions of 15.8 and 13.1 % for the first two axes.

Interpretation of the results proves to be simple, and above all focuses on axis I. The oak forests on the northern slope are situated from the origin of the coordinates towards the positive values. This main group can be split into two subgroups as a function of the axis II. The first (positive values for axis II) corresponds to the oak forests of the Sierra of Béjar and Tamames, which are neither very developed; associated with these are species such as *Phrurolithus festivus*, *Tibellus oblongus*, *Scotina celans*, *Philodromus dispar*, *Zora spinimana*, *Z. manicata*, *Clubiona compta*, and *Micaria guttigera*. The second subgroup (negative values for axis II) comprises more western oak forests, which are the most extensive and developed of the whole territory, with light and temperature conditions which clearly separate them from the rest; the species we feel to be most representative are *Clubiona neglecta*, *Anyphaena accentuata*, *Xysticus striatipes*, *X. lanio*, *X. ninnii*, *X. cor*, *X. ibex*, and *X. semicarinatus*. The oak forests of the south slope are found with negative values with respect to the first axis together with species such as *Chiracanthium seidlitzii*, *Runcinia lateralis*, *Xysticus bufo*, *Eusparassus dufouri*, *Philodromus ruficapillus*, and *P. rufus*. Differences in species composition and in the number of individuals have been reported in forests according to their degree of development or maturity (in the sense used by MARGALEF, 1974). For example, SAIZ & SALAZAR (1981) have referred to them with respect to the presence of epigeal coleopters, SAIZ & JERARDINO (1985) regarding leaf insects and FERNANDEZ-JOAQUIN (1986) with respect to epigeal spiders. The latter author also mentions fairly precise variations, within habitats of certain uniformity, related to more or less apparent structural irregularities.

The very clear-cut ordering (almost schematic) permits one to limit it to this a linear description, although between the two slopes, contact sites may be considered to exist. This is the case of «La Alberca», situated on the northern face, although it does not belong to the Duero basin but to the Tajo basin. Another case is the «Puerto de las Mezas», the pass between both slopes. As may be seen, certain nuances concerning the factors acting on the distribution of species, and on which the vegetation depends, may be added; having fixed one kind of community, the S and N exposure in this case yields distinctive aspects which are masked in the general analysis.

3. Analysis of the *Arrhenatheretea* grasslands

Similar motives that led us to study the oak forests separately, suggested the need for studying the *Arrhenatheretea* grasslands. These are developed over deep and humid soils and belong to the climatic domain of the oak. The data table comprises 27 sites $\times$ 64 species. The inertia absorbed by the first two axes is, respectively, 16.1 and 14.8 %.

Interpretation is very linear and practically resolved on the first axis which, from the positive to the negative values, reveals a descending sequence of soil humidity. Accordingly, one first finds the sites that are flooded practically all year round, with *Tibellus oblongus* and *Chiracanthium pennyi* as the main species associated. Following this are the humid grasslands exhibiting the presence of *Thanatus striatus*, *Xysticus ibex*, *X. lanio*, *X. erraticus*, *X. semicarinatus*, and *Oxyptila simplex*. Finally, the

drier grasslands are characterized by the presence of *Xysticus grallator*, *Thanatus vulgaris*, *Eusparassus dufouri*, and *Oxyptila blitea*. The effect shown by axis II seems to be apparent in precisely two of the driest grasslands in terms of the great abundance of the species *Anyphaena numida*, though it is not possible to relate this to any clear differential cause.

However, in this case, axis III (10.0% of inertia absorbed) allows one to establish nuances related again to the humid or xeric character of the communities. In this sense, two ramifications, of more humid grasslands, occur from a group close to the origin in which the drier grasslands are grouped, practically all of these belonging to the Tajo basin (S orientation of the Central System). In this sense the spider communities of the hygrophite grasslands are perfectly contrasted (positive and negative ends of axis III) as a function of geographical peculiarities, which are not shown up in axis I.

TURNBULL (1973) has pointed out that mesoclimates and microclimates tend to resemble each other more and more as the vegetation disappears (becomes clearer). In this sense it is possible that in the case of the oak forests a division might occur in terms of the slopes of the mountainous areas, attending to mesoclimatic characters (which affect the vegetation), whereas for the grasslands the relationships are more local, and depend on the hydric potential of the ground.

4. Separate analysis of the «under stone» habitat

With the sites chosen for the synecological study, by separating the under stone habitat in them, and eliminating the very rare species, a table of 168 samples $\times$ 58 species was confected. After analysis, the percentages of absorption associated with the first two axes extracted are, respectively, 9.6 and 6.6.

Figure 4 shows the projection of samples and species on the plane defined by axis I and II of the analysis. Two groups may be clearly appreciated together with a third group in which a large number of sites is situated, such that it remained undetermined in this analysis and will be studied below. It should be pointed out that diversity increases with complexity (HUHTA, 1971; JOCQUÉ, 1973; UETZ, 1975, 1976) and, in this sense, the presence of many species with no net dominance leads to results in which different communities are superimposed; interpretation is therefore extremely difficult.

The first group, situated on the positive part of axis I with both positive and negative values for axis II, corresponds to the under stone habitat of different sites sampled. The peculiar species in it are few, and most of them exhibit the same characteristic of hiding themselves in a retreat sac, either during the day (spiders with nocturnal habits) or until hatching of the eggs (in the case of certain females). Within this first group it is possible to observe a trend on the positive stretch of axis II, from lower values to the highest positive ones, defined by an abundance gradient of *Anyphaena numida*. The remaining species associated with this habitat are *Chiracanthium striolatum*, *Eusparassus dufouri*, *Liocranum majus*, *Xysticus bufo*, and *Anyphaena albirrorata*.

The second group, situated on the positive part of axis II and with values on axis I close to the origin, corresponds to shaded habitats, which owing to the kind of tree covering, are almost always shaded; these are gallery forest (*Osmundo-Alnion*) and chestnut forests.

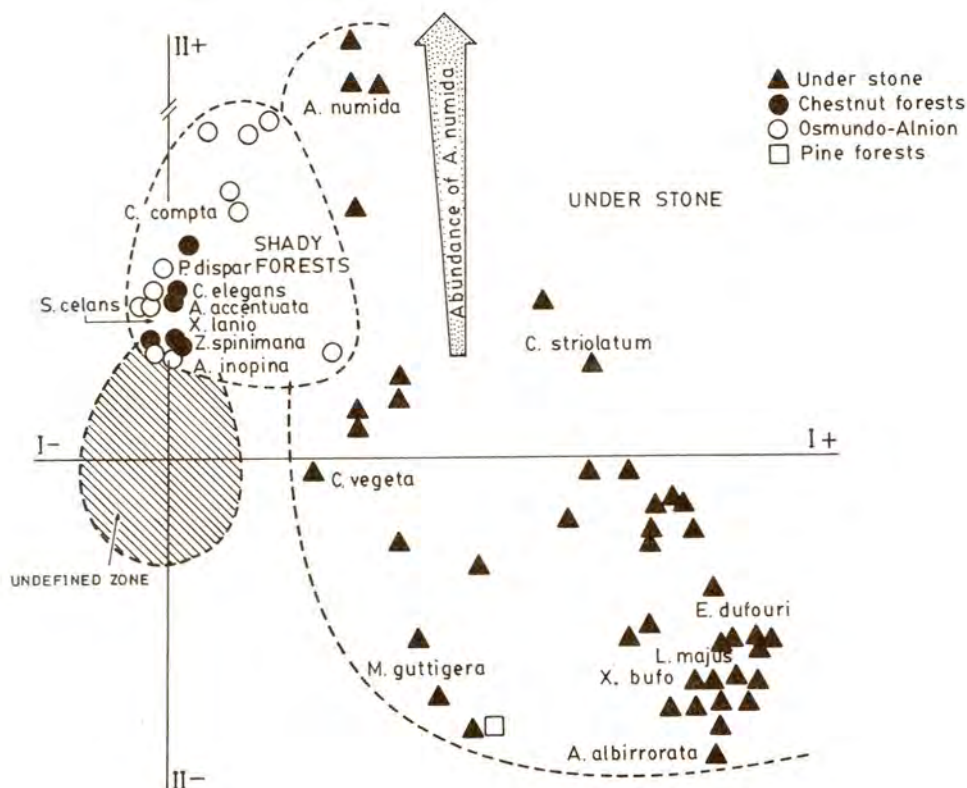


Figure 4. — Correspondence analysis separating «under stone» habitat.

Of interest in the fact that one gallery forest, situated in the Batuecas Valley, included in the holm-oak domain (class *Quercetea ilicis*), exhibits the characteristic fauna of the deciduous forests, which shows the importance for the distribution of spiders of the particular microclimate conditions, rather than the general conditions of the zone.

Within this group, some sites approach the first group; this is due to the species *Anyphaena numida*, whose life takes place in the vegetation of the shaded zones; however, at the moment of egg shedding, the spider abandons this habitat and hides under stones with its egg bag.

The characteristic species of these shady woods are several; outstanding among them are *Philodromus dispar*, *Clubiona compta*, *Anyphaena accentuata*, *Xysticus lanio*, and *Chiracanthium elegans*.

5. Analysis of the group undefined in the first results obtained on considering the «under stone» habitat separately

With the third group of the previous analysis, whose interpretation offered certain difficulties, we carried out a new separate analysis (table of 105×58 species). The percentages of inertia associated to the first two axes were, respectively, 7.8 and 6.1

Figure 5 shows the ordering of the sites and species along the first two axes. As may be seen, the first axis defines a gradient of soil humidity from the lowest negative to the highest positive values. In this group, and around the origin, are found the humid grasslands which may be included in the class *Arrhenatheretea*, the mountain grasslands of the class *Nardetea* and the shallow bog-pool zones of the class *Oxycocco-Sphagnetea*; close to these sites the species *Thanatus oblongiusculus*, *Xysticus semicarinatus*, *Oxyptila simplex*, *Xysticus striatus*, and *Chiracanthium puncturum* can be found. The highest values on axis I belong to a group of sites characterized by their high degree of soil humidity and great altitude, above 1000 m; associated species found are *Chiracanthium pennyi* and *Tibellus oblongus*.

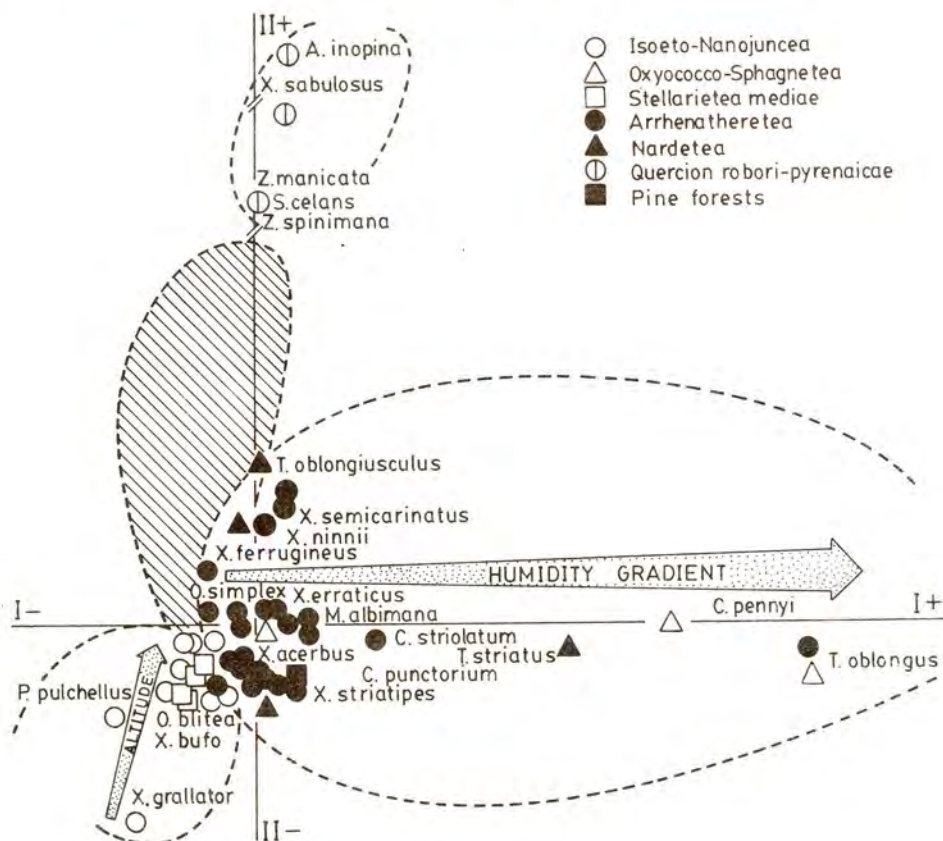


Figure 5. — Correspondance analysis with the undefined group of the previous analysis (fig. 4).

Continuing along the negative part of axes I and II, a group of sites appears, situated on the southern slope of the Sierra and whose vegetation belongs to *Isoeto-Nanojuncetea* and *Stellarieta mediae*, which exhibit the common characteristic of being humid in spring but almost completely dry in summer. Within this group of sites it is possible to observe an altitude gradient, the lower altitude sites and those closest to the origin being situated in the higher values of the negative part of axis II. The indicative species of this group are *Xysticus grallator*, *X. bufo*, *Oxyptila blitea*, and *Philodromus pulchellus*.

In the contact zone between the two groups, where the characteristics of one and the other become mixed, there is a certain overlap.

Towards the more positive value of axis II are found the oak forest of the Sierra of Béjar, with an altitude ranging between 1200 and 1300 m a.s.l.; the characteristic species are *Agroeca inopina*, *Scotina celans*, *Zora manicata*, *Z. spinimana*, and *Xysticus sabulosus*.

Finally, between these three groups, on axis II and with values around the origin of axis I, lie the rest of the sites. These are practically superimposed and no definite trend can be distinguished between them, since they have varying vegetation, which can be included in different classes, and the number of species present in them is high. When a further partial analysis was conducted no interpretable ordinations were observed.

Conclusions

The reciprocal averaging technique provides confirmation of aspects reported in autoecological studies and at the same time allows one to establish certain nuances; above all, it provides an overall sense to the study conducted.

In view of the fact that it is the result of all the prevailing environmental factors, vegetation is logically related to the spider populations. However, to this it should be added that the effects of vegetation (shaded and sunny sites) and certain determinant causes of their presence (exposure, soil humidity, altitude) can be considered alone, without taking other aspects into account, as long as one works under conditions of certain uniformity with respect to the remaining factors.

The «under stone» habitat shows a pronounced degree of independence, and has species of its own. In fact, one could speak in terms of a macroclimate, a mesoclimate and a microclimate, which affect species composition in very different ways since although the first affects general conditions (limit of habitat possibilities, indirect influence on the spiders). Accordingly, the microclimate is very manifest in the enclaves situated under the stones but the development of activities may depend more on the mesoclimate of different plant formations; for example, the presence of the same species in shaded forests, chestnut forests and river-side gallery forests indicates a manifest mesoclimatic convergence.

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