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On the biogeography and faunistics of European spiders: latitude, altitude and insularity

par
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Summary: The number of spider species known from small central European countries or areas (30–40 thousand sq.km) varies from 600 to 875, the highest being in Switzerland. In the more northern, small and flat areas, Denmark and Estonia (ca. 45 t.sq.km), 510–520 species are found. In larger central European countries (70–550 t.sq.km) 600–1400 species are known, of these the lowest numbers are from the somewhat isolated Great Britain and the highest from France. In northern Europe, large Fennoscandian countries (320–410 t.sq.km) have 535–695 species. About 2200 species are known from the huge USSR (22 402 t.sq.km); of these 940 from the Russian plain.
In well-studied small areas, a markedly high number of species can be found, e.g. 511 (55 % of the total German fauna) in West Berlin and 425 (67 % of the Finnish fauna) at Tvärminne. The areal size is less important than the latitude, altitude and isolation. An increase in each of the latter has the effect of decreasing the richness and diversity of spider fauna; the family Linyphiidae (s.lat.) being dominant in extreme high, northern or insular conditions in Europe. The number of species in Slovenia (46°N) and Inari Lapland (69°N), areas of equal size (20 t.sq.km), are 530 and 220 respectively.
Of ecological islands on mainland, high mountains and raised bogs offer a site for northern relicts, warm slopes and cliffs and, to some extent, caves for southern species.
Environmental problems, especially in densely populated areas of Europe, have brought out the need for accurate faunistic data on rare, endangered species (and on their endangered habitats which are often ecological islands on mainland). A common European mapping program of spiders, e.g. using UTM squares of 50 x 50 km, would be very welcome for both biogeographical and conservation studies. Naturally, it is not possible to begin this mapping without intensive cooperation between specialists of all countries and without a center for the practical compilation work.

1. INTRODUCTION

Nature in Europe, including its spider fauna, has been greatly affected by the Ice Age. The ice sheet covered northern Europe during the last glaciation and its retreat, about 15 000 – 8000 years ago, started, in northern Europe a successional development of different ecosystems from tundra deserts to the recently occurring ones. The effect of the Ice Age on the spider fauna of northern and central Europe is well–known and easy to understand. However, the glaciation also affected the southern, Mediterranean spider fauna (e.g. BRIGNOLI 1981).

When considering the European spider fauna and its development after the glaciation, some debated concepts must be mentioned. The connections with eastern (Siberian–Alaskan) and western (North American) areas have been much discussed. Because of large ice–free areas in Siberia connected with the Beringian land bridge to ice–free parts of Alaska, marked faunal migration from Beringia could be expected (e.g. GORODKOV 1984), especially in tundra and taiga forest zones of Europe. The possibility of North Atlantic land bridges has been also discussed (LINDROTH 1957), but they seem to be very improbable and the faunal resemblance must be explained otherwise. Ice Age refugia are also interesting and much treated phenomenoms (e.g. LINDROTH 1969, ASHMOLE 1979). The recent range of certain plants and animals could often be explained nicely by small–sized refugia (nunataks or coastal refugia), surrounded by ice sheet. The importance of small–sized refugia seems to be more favoured in North America than in Europe today (see e.g. PIELOU 1991). The occurrence of large–sized refugium areas is commonly accepted (e.g. BRIGNOLI 1981; MAURER & THALER 1988).

The natural expansion routes for the fauna of postglacial Europe were from the east, southeast and south. Within Europe, different faunal elements spread northwards and so the recent spider faunas seem to be of mixed origin. One could expect that the spider fauna of Finland, at the western end of the taiga forest zone, would be rather similar to that in Yakutia, eastern Siberia. However, only about 40 % (150 species) of the Yakut species (about 400 species known, MARUSIK et al. unpubl.) are found in Finland; for comparison, about 75 % (450 species) of the Finnish and British spiders are in common (ROBERTS 1987, LEHTINEN et al. unpubl.).

The ice sheet disappeared in northernmost Europe less than 10 000 years ago. Thus, we could think that the spider fauna of northern areas is still developing and that not all potential species have arrived. Spiders are effective in dispersal, especially species using ballooning. For example, within seven study years five species reached the new volcanic island of Surtsey near Iceland; area of about 2.5 sq. km. All were linyphiids (s. lat.); four occurring in Iceland but one probably arrived from the British Isles (LINDROTH et al. 1973). CRAWFORD (1985) found 43 species of spiders in a totally destroyed and vegetation–free site at Mount St. Helens, Washington, one and two years after the devastating eruption. They all belonged to groups known to be ballooners. MEIJER (1977) studied immigration into a new polder in the Netherlands during a period of four years. More than 80 species were found and about 20 of them were regarded to have established populations in the area (MEIJER 1977). Ballooning groups have probably reached in the north the areas where they can live, but for non–ballooners it is not always clear. Naturally the spider faunas are dynamic and changing, basically due to climatic changes. There are several recent immigrants from the European continent over the Channel to the British Isles; partly probably caused by man (e.g. HAMBLER & LINFIELD 1991).

2. AREA, LATITUDE AND ALTITUDE

The number of spider species known is naturally higher in southern areas than in the north (table I). In Central Europe, 600–850 species can be found in an area of 30 000 – 40 000 sq. km. The effect of latitude and altitude can be seen in the species numbers of Switzerland (875) and Denmark (510), both about 40 000 sq. km. Latitudinal effect may explain the difference in numbers between nearly equal–sized Holland (605) and Denmark (510), both countries being flat. The great number of islands belonging to Denmark may also be a reducing factor in species number. Sweden, Norway and Finland are rather large countries, but due to their northern situation, the species numbers are rather low (535–695). The species number in Holland and Finland is equal (605); the area of Finland being tenfold that of Holland. On the other hand, isolation from the European continent causes the lower species number in Great Britain (620, i.e., less than in Belgium on the other side of the Channel). In addition, the spider fauna of Great Britain has been studied thoroughly by both amateurs and professionals and is thus very well–known. The species number in large countries (Germany 925, Sweden 695, France 1400, Russian plain 940, USSR 2200 species) is not naturally directly correlated with the area. It is not possible to investigate wide areas in as detailed a way as the smaller ones.

The size of a study area (country, province etc) is not very important when dealing with the number of species to be found. Thus PALMGREN (1972) reported 425 species (70 % of the Finnish fauna) from the surroundings of the Tvräminne Zoological Station, southern Finland, and PLATEN et al (in press) as many as 511 from West Berlin (480 sq. km; 55 % of German species) (table II). It must also be borne in mind that both Tvärminne and Berlin are lowland areas without mountains.

Tab. I. - Approximate number of spider species known from different European countries/areas; 1: number of species; 2: area (1000 square km), * : ice–free area; 3: species/1000 sq. km; 4: maximal altitude (m); 5: reference.

	1	2	3	4	5
Slovenia	530	20.2	26.2	2863	NIKOLIC & POLENEC, 1981
Belgium	645	30.5	21.1	690	BOSMANS & MAELFAIT, 1986
Netherlands	605	33.9	17.8	320	VAN HELSDINGEN, 1988
Switzerland	875	41.2	21.2	4630	MAURER & HÄNGGI, 1990
Pyrenees	860	~40	21.5	3404	BOSMANS & DE KEER, 1986–87
Baden–Württemberg	670	35.7	18.8	1493	RENNER, unpubl.
Denmark	510	43.1	11.8	170	BØGGILD, pers. comm.
Estonia	516	45.1	11.4	317	VILBASTE, 1987
Bavaria	750	70.5	10.6	2960	BLICK, unpubl.
"DDR"	705	108.3	6.5	1220	MARTIN unpubl.
Czechoslovakia	860	127.9	6.7	2650	BUCHAR, pers.comm.
England & Wales	600	151.2	4.0	1085	ROBERTS, 1987
Great Britain	620	230.7	2.7	1340	ROBERTS, 1987
Alps	1000	~240	4.2	4810	THALER, 1980
Romania	850	237.5	3.6	2540	WEISS, 1988
"BRD"	855	249.5	3.4	2960	BAEHR & PLATEN, pers.comm.
Poland	740	312.6	2.4	2500	WOZNY, 1985
Germany	925	357.8	2.6	2960	PLATEN, pers.comm.
France	1400	551.0	2.5	4810	JONES et al., 1990
Norway	535	323.9	1.6	2470	HAUGE 1989
Finland	605	338.1	1.8	1324	LEHTINEN et al. unpubl.
Sweden	695	411.5	1.7	2123	KRONESTEDT pers.comm.
Russian plain	940	~2000	0.5	(low)	MIKHAILOV pers.comm.
USSR	2200	22402	0.1	7495	MIKHAILOV pers.comm.
Shetland	90	1.4	64.3		ASHMOLE 1979
Faroes	67	1.4	47.9		BENGTSON & HAUGE 1979
Svalbard	14	8.0*	1.8		TAMBS–LYCHE 1967
Iceland	90	89.7*	1.0		ENCKELL 1985
Greenland	69	341.7*	0.2		KOPONEN 1982

Tab. II - Composition of the spider fauna of certain well–studied sites at different latitudes. 1: number of species, 2: percentage of linyphiids s.lat., 3: number of families, 4: reference.

	1	2	3	4
Isfjord, Svalbard (78°N)	13	93%	2	HOLM 1958
Kevo, Finland (70°N)	164	77%	18	KOPONEN 1984
Tvärminne, Finland (60°N)	425	42%	24	PALMGREN 1972
Berlin W, Germany (52°N)	511	36%	33	PLATEN et al. in press

Tab. III - Number of families (according to PLATNICK 1989) in certain countries/area

World	105	(PLATNICK 1989)
USSR	46	(MIKHAILOV, pers.comm.)
Switzerland	39	(MAURER & HÄNGGI 1990)
Russian plain	36	(MIKHAILOV, pers.comm.)
Belgium	35	(BOSMANS & MAELFAIT 1986)
Great Britain	35	(ROBERTS 1987)
Norway	29	(HAUGE 1990)
Finland	27	(LEHTINEN et al. unpubl.)
Shetland	12	(ASHMOLE 1979)
Iceland	10	(ASHMOLE 1979, EINARSSON 1984)
Greenland	10	(HOLM 1967, KOPONEN 1982)
Svalbard	2	(HOLM 1958, TAMBS-LYCHE 1967)

The spider fauna in the northern areas is less rich and less diverse than that in the south (table III).

The family Linyphiidae (s. lat.) is dominating in species numbers when moving northwards (table II). The opposite is true for many other families, such as Salticidae, where the species number from southern Europe (40–45°N) to the North (66°30'N) decreases from 88 to 11 (PROSZYNSKI 1978). Some families have the northern limit of their range near the southern coast of the Baltic Sea (e.g. Zodariidae) and several have barely colonized the southernmost part of Sweden and/or Norway but are absent from most of these countries, as well as totally absent from Finland, for example, Atypidae, Uloboridae, Oonopidae, Dysderidae and Theridiosomatidae.
The effect of latitude is shown when comparing the species numbers of two equal–sized (20 000 sq.km) areas: Slovenia (46°N) and Inari Lapland (69°N). The number of known species in Slovenia is 530 and in Inari Lapland 220 (NIKOLIC & POLENEC 1981, KOPONEN 1984 and unpubl.).

The effect of altitude can be seen best on mountains which are islands surrounded by lowlands. Great mountain areas of Europe, such as the Alps, the Carpathians and the Pyrenees have their special fauna with a high number of endemic species. For example, BOSMANS & DE KEER (1986–87) regarded 12 % of the found 860 Pyrenean species as endemics. The biogeography, including endemism, of the spider fauna of the Alps has been studied intensively by THALER (e.g. 1980) and MAURER & THALER (1988). The endemic species can be found in different altitudal zones in the mountains; in the Pyrenees they were common in subalpine and especially montane forest zone sites (BOSMANS & DE KEER 1986–87).
At high altitudes the number of species as well as of families decreases (as towards the north). Thus, in Switzerland, the number of species and families occurring in all altitudal zones is 21 and 9 respectively, and that of species restricted to alpine–nival zones is 13 and 4 (MAURER & HÄNGGI 1990); altogether 11 families in alpine and nival zones. In the East Alps, THALER (1988) found 49 species belonging to 7 families from the nival zone. In the Pyrenees, 52 species and 12 families of alpine and arctic–alpine species were found (BOSMANS & DE KEER 1986–87). In northernmost Sweden, the Torneträsk area, nine species of two families (eight linyphiids s. lat. and one lycosid) were found in the high alpine zone, above 1300 m; and 14 species of three families occurred only in the alpine zone, above 600 m, although as many as 80 species were altogether observed in the alpine zone (HOLM 1950). The families dominating at a high altitude in Europe are linyphiids (s. lat.), lycosids and gnaphosids.

3. INSULARITY

3.1. Ecological islands

The occurrence of northern (relict) species in the Central and South European mountains is well–known. MAURER & HÄNGGI (1990) listed 30 arctic–alpine and boreal–subalpine species from Switzerland, and BOSMANS & DE KEER (1986–87) 14 arctic–alpine from the Pyrenees. Arctic–alpine species have been reported, in smaller numbers, e.g. from the High Tatras in Czechoslovakia (SVATON 1983) and the Pirin Mountains in Bulgaria (DELTSHEV 1990).
However, the spider communities at high altitudes in the Alps and, e.g. in northern Fennoscandia, differ. Thus PALMGREN (1973) reported that only three of the most abundant 15 sublapidicolous alpine spiders at Kilpisjrvi, Finnish Lapland, were among the abundant sublapidicolous species in the nival zone of the East Alps. At least for some arctic–alpine species the habitat requirements become more eurytopic in the north. For example, *Tiso aestivus* occurs in Switzerland in the alpine and nival zone (above 2300 m; MAURER & HÄNGGI 1990), has been found in the subalpine and alpine zone at Torneträsk, Swedish Lapland by HOLM (1950); and is typical in the alpine zone at Kevo, northernmost Finland (where the alpine zone begins at 300 m), but can be found there also at man–made open sites in the forest zone (KOPONEN 1988).

Mountains offer an island for northern spiders in the south, as do raised bogs: the occurrence of northern plant and animal species on bogs has been known for a long time. PETERSEN (1954) presented the concept 'mire species' for them. Typically, these mire species occur in the southernmost part of the range only on bogs and in the north they are more eurytopic. This has been found in spiders as well, e.g. *Pardosa hyperborea*, *Gnaphosa lapponum, G. microps* and *Robertus lyrifer* are found in southern Finland only on peat bogs and in Finnish Lapland these species are markedly eurytopic. The same phenomenon is true for the bogs of Central Europe. Bogs are very threatened biotops, many of them have been dried; so that even in Finland, where 30 % of the land was regarded as bogs in the 1950's it is now difficult to find large natural bogs in the southern part of country. The effect of drying is well–known: the specialized bog species disappear and more eurytopic species become abundant (KOPONEN 1979).
Islands for both thermophilous and hygrophilous species are also rocky slopes (stony debris) where some rare relict species have been found, e.g. the Siberian linyphiid *Wubanoides longicornis* in Czechoslovakia (RUZICKA 1990). Warm slopes and cliffs offer an island for many southern thermophilous species, especially in Central Europe (e.g. STEINBERGER 1988) but also in the north. On the other hand, shaded moist cliffs are sites for northern species.
Nowadays natural forest habitats have became widely scattered in populated areas. And even in northern Europe, e.g. in Finnish and Swedish Lapland natural primeval forests has been reduced greatly during recent years. Although there seem to be only a few if any species restricted to boreal primeval forests (VÄISÄNEN & BISTRÖM 1990) they are optimal biotops for many spiders, especially linyphiids.
Caves are a special environment, patchily distributed or insular, with often very specialized spider fauna. Obligate cave–inhabitants, troglobites, are strongly adapted to living in caves. Troglobites occur in caves of southern Europe, mainly around the Mediterranean Sea. Typical groups are blind dysderids and linyphiids (*Troglohyphantes* and *Centromerus*) and some leptonetids (DEELEMAN–REINHOLD 1981). An extraordinarily high number of blind spiders is known from SW Yugoslavian caves compared to the surrounding areas, such as East Serbia, Greece, Bulgaria and Italy. For example, more than ten blind or semiblind species of the *Troglohyphantes salax* group have been reported from Yugoslavia and only one from nearby Bulgaria (DEELEMAN–REINHOLD 1981). Specialized troglobites occur commonly also in the Pyrenees and on some Mediterranean islands. In northern Europe, troglophilic species are typical. They have successfully colonized widely scattered caves, so that e.g. *Meta menardi, Metellina merianae, Nesticus cellulanus, Porrhomma convexum* and *Lepthyphantes pallidus* can be found at the Arctic Circle in Norway (HIPPA & KOPONEN 1988). In general, the total number of spiders found in caves in northern areas is not markedly smaller than that in southern Europe, except perhaps in some particular karstic areas; e.g., 61 species from seven caves in Scandinavia vs. 76 from 410 Bulgarian caves (HIPPA et al. 1984, DELTSHEV 1983). BRIGNOLI (1972) listed 177 species from Italian caves.

3.2. North Atlantic islands

The number of species (and families) decreases strongly when moving from the main islands of Britain or from Scandinavia to the North Atlantic islands (table I). The faunas of both Shetland and the Faroes are equally similar with those of West Scandinavia (Norway) and the Scottish mainland, but the fauna of Iceland resembles more Scandinavian than Scottish faunas (ASHMOLE 1979, ENCKELL 1985). In general, the Nearctic element (probably via Greenland) is small; some Icelandic species can be mentioned. Of these, the lycosids *Pardosa furcifera* and *P. groenlandica* were found in large numbers in the nineteenth century, but seem to be extinct now (BRAENDEGAARD 1958, ASHMOLE 1979). The fauna of Greenland consists of Holarctic (40 %), Nearctic (40 %) and Palaearctic (20 %) species (HOLM 1967, KOPONEN 1982). In Svalbard, the majority of the species are circumpolar (HOLM 1958).

When comparing two arctic study sites, Isjford in Svalbard (HOLM 1958) and Hazen Camp in the Ellesmere Island (LEECH 1966) the main difference is the family number (table IV). Only two indigenous families (12 Linyphiidae and one *Micaria* species) were found in Svalbard but four families (9 Linyphiidae, 2 Lycosidae, one Dictynidae and Thomisidae species) in the even more northern Ellesmere Island; the total number of species being 13 at both sites. The main factor seems to be the isolation: the distance from Svalbard to Greenland is 450 km, to Scandinavia 700 km and to Novaya Zemlya 900 km. In the Canadian high arctic archipelago the sounds are much narrower (ca. 100 km).

Tab. IV - Comparison of the faunas of two arctic sites, Isfjord in Svalbard and Hazen Camp in Ellesmere Island.

	Isfjord	Hazen Camp
Number of species	13 (+2 introd.)	13
Number of families	2 (+1 introd.)	4
Latitude	78 °18'–30'N	81°49'N
Total area of island	65 300 sq.km	198 100 sq.km
Ice–free area	8 000 sq.km	117 600 sq.km
Isolation, distance	450–900 km	~100km

4. HUMAN INFLUENCE: ENDANGERED SPECIES

In some countries spiders have been included in "Red Books" as endangered species, and in many countries especially in Central Europe, this listing is being done. For example, in Finland (ANON. 1985), 27 species of spiders (ca. 4 % of fauna) were included, and two of these were listed as extinct species (e.g. *Agelena labyrinthica*). In Sweden, three species (*Atypus affinis, Araneus nordmanni* and *Hyptiotes paradoxus*) were included in the list of endangered species of Swedish woodlands (EHNSTRÖM & WALDEN 1986). MARTIN, PLATEN & SACHER (in prep.) regard 12 species as extinct and 25 more as highly endangered in Germany.

When dealing with the whole European spider fauna, the term endangered species varies very much in different areas (countries). Thus species listed in the Red Books in northern Europe may be commonly found in more southern regions. Although local lists of endangered species may be based on different levels of knowledge and on different opinions concerning the threat, they offer valuable information about rare species and often about their special habitats which should naturally be protected and not the species as such. Although DUFFEY (1974) reported that only one or two native British spiders had been lost by the land–use changes and no more seemed to be in actual danger, the present situation in densely populated areas of Europe seems to be markedly worse. The species of small–sized ecological islands (e.g. bogs) are endangered in particular.

A common European mapping system for spiders, such as the European floristic survey publishing 'Atlas Florae Europaeae', could give the basic data for conservation work. This kind of mapping (e.g. using 50 x 50 km UTM–squares) would be very welcome, but it will also be very demanding and time–consuming work. Local mapping programs are already at work in many countries, e.g. the Spider Recording Scheme in Great Britain (e.g. SMITH 1990).

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