

Regional variation of habitat tolerance by some European spiders (Araneae) – a review

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Abstract: The data presented by HÄNGGI et al. (1995) and BOLAÑOS (2003) on the habitats of a large number of European spiders are examined, most of which appear to show non-specific preferences. The abundance and frequency peaks of the 384 species graphs (HÄNGGI et al. 1995) can be explained by assuming that habitat tolerance varies with geographical location. This can be demonstrated on a local level within a particular country or throughout the European range of a species. Examples are described. Many published ecological studies of spider faunas seem to have assumed that the habitat preferences of a species is a fixed characteristic wherever they occur but evidence is presented to show that this may apply to only a few species. A number of examples are described showing how preferences change with latitude and longitude within Europe. It is proposed that most species can be categorised as stenotopic, mesotopic or eurytopic, although there is a gradual change from one group to another, with no clear boundaries. Supporting evidence for regional variation in habitat tolerance is scarce.

More studies are required of individual species throughout their European distribution and detailed descriptions of their habitats in different parts of their range. Definitions of micro-, macro- and minor habitats are presented as useful tools for field studies of spider faunas. It is also recommended that future faunal surveys should use the same system of habitat classification so that the results are comparable with other studies. The most appropriate method is described by BUCHAR & RŮŽIČKA (2002) but could be made more precise by the use of scientific measuring equipment for light/shade, dryness/humidity and temperature. Finally the importance of checking the validity of some published records is stressed because misidentifications are sometimes frequent.

key words: Araneae, habitat classification, habitat tolerance, species distribution

There have been many advances in our knowledge of the field ecology of spiders in recent years but we still know very little about the range of variation in habitat tolerance throughout a species' geographical range. Do species associated with a particular habitat in one region demonstrate the same preferences elsewhere? Some species seem to be able to adjust to a wide range of different habitats while others are usually restricted to the same environmental conditions wherever they occur. Between these two extremes can the pattern of variation in habitat choice be classified?

An analysis of habitat data recorded for many European spiders was made in the pioneering work of HÄNGGI et al. (1995). They used 223 literature sources, including 1382 species lists, from which they selected 384 species which could be allocated to a classification of 19 major habitat groups divided into 85 preselected minor habitats. Most of the records, 58%, came from Switzerland, Germany and Austria but some British, French and Scandinavian

data were included, resulting in a wide geographical spread. For each of the 384 species graphs were prepared of abundance and frequency plotted against the habitat categories. The remaining 554 species are presented in a separate list.

Their results are of very considerable interest but seem to show that for many species there is no clear preference for a particular habitat or group of related habitats. BOLAÑOS (2003) comments that most of the species seem to have 'non-exclusive or non-specific habitat preferences'. In an attempt to obtain more precise conclusions he selected those studies used by HÄNGGI et al. (1995) which collected ground-living spiders in pitfall traps from locations below 800 m altitude and confined to central Europe. His analysis of the data selected clusters of species revealed by a multi-variate statistical package which defined the type of habitat with which the clusters were associated. Species which did not show a clustering response were eliminated. This interesting but highly selective approach resulted in 19 clusters which could be matched with habitats which were mostly defined in terms of vegetation.

These two studies are valuable contributions to the subject of habitat choice by spiders though in each case it was difficult to achieve 'clear-cut' conclusions. The authors were well aware of the limitations of the data available to them, especially the variation in collecting methods, duration of study and the inadequacy, in many cases, of habitat recording. In addition there was the unknown factor of combining records from many geographical locations in Europe, in each of which the spiders were reacting to different environmental influences. However, HÄNGGI et al. (1995) suggest that 'the same microhabitats may exist in different macrohabitats'. The implication of this is that a species may be recorded from several apparently very different habitats but in each one similar ecological niches are present, so that the species is able to survive. Nevertheless when the habitat choices are plotted on a graph in relation to a conventional habitat classification such a species appears to tolerate a broad range of environmental differences and would be labelled as having non-exclusive habitat preferences.

The definition of habitat and related terms

The word 'habitat' is used frequently in this paper so it is necessary to examine precisely what it means in the context of regional variation in habitat tolerance. In addition other terms such as 'macro-' and 'microhabitat', 'major and minor habitat', 'biotope' and 'ecological niche' will be discussed.

There is general agreement in the seven ecological dictionaries consulted that a 'habitat' describes the place and environment of a particular species. However, habitat classification schemes are based on vegetation and the physical components of the environment without regard to the influence of the animal community so that the concept of a habitat is mainly concerned with its structure. This is inevitable on present knowledge but the ecological niche (or niches) of a habitat is of equal importance to the subject of this paper.

In most ecological studies the term habitat is used in a very general sense and may describe a simple environment or else a large and complex system. This account includes references to both types and it is necessary to define the meaning of the terms used for different subdivisions of habitats.

Microhabitat

This term is widely used and defined in most ecological dictionaries. LINCOLN et al. (1998) describe it as 'a small specialised habitat'; RAMADE (2002) as 'habitat de très faible étendue et spécialisé' and SCHAEFER & TISCHLER (1983) as 'allgemein ein Kleinlebensraum mit geringer räumlicher Ausdehnung'. Examples quoted are: twigs, leaves, tree bark crevices, the different plant structures, dung, nests, etc. Other dictionaries concur and this meaning is followed in this account.

Macro-, major and minor habitats

None of these terms are defined in the seven ecological dictionaries available to me, although they are used in some publications. I have assumed that macro- and major habitats are identical and both are used in this paper in order to reduce repetition. They refer to large-scale homogeneous entities such as a heathland, deciduous or coniferous forest, extensive marsh, coastal dune system, or a grass plain. It is also useful to consider a comparative term for a habitat which is neither macro- nor micro. The term 'minor habitat' could be used to describe formations such as a copse or hedgerow, a shrub margin to a forest, a pond or a stream, disused gravel, sand or stone pits and some other man-made habitats such as mines, culverts, buildings. In the habitat classification of HÄNGGI et al. (1995) the 19 subdivisions are called major habitats and the 85 smaller subdivisions are regarded here as minor habitats.

Ecological niche

It is not possible to describe the habitat of a species without some reference to how it lives and adapts to its environment together with competitors, predators and parasites. ODUM (1971) described the habitat of a species as its 'address' and its ecological niche as its 'profession' to illustrate the relationship.

RAMADE (2002) defines this term as 'la place et la spécialisation d'une espèce à l'intérieur d'un peuplement. Dans tout écosystème il est fréquent que de nombreuses espèces se rencontrent dans un même habitat voire occupant des micro-habitats très voisins sinon identiques. En revanche, une étude détaillée de leur biologie confirme qu'elles occupent chacune une niche écologique bien distincte.' Both LINCOLN et al. (1998) and SCHAEFER & TISCHLER (1983) summarise the definition as 'the ecological role of a species in a community'. The term 'community' is defined by most ecological

dictionaries as all the organisms interacting together at all trophic levels in the ecological niche and not as incorrectly used by many authors who refer only to a population of related animals such as the order Araneae.

Ecological niche in this paper follows the above description.

Biotope

This term is not used because definitions vary in the seven ecological dictionaries consulted and there may be confusion with 'microhabitat' in the context of this paper.

Regional differences in habitats selected by spiders

If spider species originally evolved in relation to specific habitat or environmental conditions, some would continue to be confined to a narrow range of niches while others would adapt to a greater diversity and so become more common and widespread. Many of the graphs of HÄNGGI et al. (1995) may show an advanced stage of the latter process. These species became successful by the ability to exploit different environments but we need to examine how their habitat preferences change from one region to another. A few examples follow which try to illustrate the complexity of this aspect of spider ecology. Data are few because the available field records are insufficient or inadequate. Three categories of habitat tolerance by spiders are presented, stenotopic, mesotopic and eurytopic.

'Stenotopic' and 'eurytopic' are defined in most ecological dictionaries/encyclopaedias. CALOW (1999) says that 'stenotopic' 'describes organisms that are only able to tolerate a narrow range of environmental conditions and hence have a very restricted distribution'. LINCOLN et al. (1998) agree but use 'habitat' instead of 'environmental conditions'. RAMADE's (2002) definition is similar.

Although I use 'stenotopic' in the same way, I do not agree that tolerance of a narrow range of environmental conditions (or of habitats) necessarily leads to a very restricted geographical distribution. The particular conditions of the habitat may be very specialised but, in some cases, can also be widespread; see *Philodromus fallax* below.

'Eurytopic', the opposite of 'stenotopic', is defined in ecological dictionaries as 'tolerant of a wide range of environmental conditions (or habitats)' and, in this case, is usually characterised by a wide geographical distribution.

'Mesotopic' is not defined in any ecological dictionary or encyclopaedia available to me. However, this term clearly describes, in a comparative sense, a habitat tolerance which fits those species neither 'stenotopic' nor 'eurytopic', though further explanation may be necessary for each case described.

Stenotopic species

These species are restricted to the same or similar environmental conditions wherever they occur. Strict stenotopy is probably rare because the more we learn about the behaviour and ecology of spiders, the more we find that many species, unless very localised, are able to survive in a wider range of environments than previously recorded.

Philodromus fallax was the only species out of 384 selected by HÄNGGI et al. (1995) for their graphs that was recorded from only one major habitat (sandy beaches, coastal dunes). From the Atlantic coast of temperate west Europe to Scandinavia and the German North Sea coast (SCHULTZ & FINCH 1996) it is reported from only this type of environment. However, much further east, in the Tuva Province of south-central Siberia, it is well-established in terrestrial habitats far from any coastline (MARUSIK et al. 2000, Logunov & Koponen pers. com.). In this area it has been recorded by lake shores, some of which are saline, on dry sandy soil among tussocks of the grass *Achnatherum splendens*. The lake levels rise during periods of heavy rain and the surrounding land may be flooded. *P. fallax* has also been taken in closed-sward meadows and amongst scattered vegetation on the pebble banks of rivers in the same region. Some of the habitat described appears to be structurally similar to the *Ammophila arenaria* dunes of northwest Europe but the seasonal temperature range is probably very different.

Some other species typical of marine environments show marked stenotopic preferences. *Halorates reprobis* is restricted to Ireland, British Isles, Iceland, Belgium, Netherlands, northern France, Germany and Scandinavia in Europe. It occurs on rocky shores in marine algae and on salt marshes. *Arctosa fulvolineata* is only recorded from France including Corsica, Italy including Sardinia, Spain, Portugal and Britain, usually under stones and in cracks in dried mud on salt marshes and estuarine marshes. Published inland records for this species have been shown to be misidentifications. *Erigone arctica*, a more widely distributed species, is also typical of salt marshes, beach driftlines and

coastal dunes, and is sometimes very abundant. In Scandinavia it also occurs on stony mountainsides (HOLM, 1950, HAUGE, 1977) and (in Britain) in flooded gravel pits, inland saline areas, and the filter beds of sewage treatment works (BRISTOWE 1939 & 1941, HARVEY et al. 2002, DUFFEY 2004). It is usually scarce or much less numerous in the minor terrestrial habitats. *E. arctica* appears to be only loosely stenotopic but the graph of HÄNGGI et al. (1995) shows that approximately 88% of records are from coastal areas, 10% from inland habitats with fresh water, and 1.8% from mountains.

Similar stenotopic characteristics are found in some species typical of mountains, for example *Lepthyphantes whympersi*, *Erigone tirolensis* and *E. psychrophila*. In the far north some mountain species may be found at low altitudes where the habitat is similar to mountain environments. In wetlands the habitats are often very variable and good examples of stenotopic species are still sought. However, the fen spider *Hypomma fulvum* is interesting because it has a strong preference for reed swamps (Phragmitetum or Cladietum), though there are records for wet grassland, sedge tussocks, fen woodland and raised bogs. DUFFEY (1991) showed that in East Anglia, England, it was more common in reed beds close to the coast than further inland. In 7 other European countries reed beds are mentioned as one of the preferred habitats for *H. fulvum*.

The transition to mesotopic characteristics is gradual and there is no clear boundary between stenotopism and mesotopism.

Mesotopic species

This category of species may show a wider tolerance of different habitats but there is usually a clear association with certain environmental conditions often illustrated in the HÄNGGI et al. (1995) graphs by one or two high abundance peaks for a particular habitat or habitats (Tab. 1). In some species their preferences may be hidden if similar niches occur in different habitats.

Zelotes electus, in Britain, is almost entirely confined to coastal sand dunes though it has been recorded on two inland sandy areas (HARVEY et al. 2002). HÄNGGI et al. (1995) record a high abundance peak for sandy coasts but there are also records for oligotrophic grasslands, heaths and vineyards. BUCHAR & RŮŽIČKA (2002) record this species 'under stones on rock steppes' and MIKHAILOV & MIKHAILOVA (2002) found it at 2500 m in the Caucasus mountains. MAURER & HÄNGGI (1990) record it from dry places, gravel pits and hay meadows in Switzerland. Although these environments appear very different all may have similar microhabitats characterised by openness, dryness and warmth.

Agroeca cuprea, in Britain, is mainly confined to a few south coast dune systems and inland dry

Tab. 1: Eleven mesotopic species taken from the graphs of HÄNGGI et al. (1995). All have one or two abundance peaks for a particular habitat or habitats and also occur in several other macrohabitat categories.

Species	Habitats with abundance peak(s)	Representation in the 18 other macrohabitats
<i>Argenna subnigra</i>	Coastal dunes	5
<i>Euophrys aequipes</i>	Oligotrophic grassland	12
<i>Haplodrassus umbratilis</i>	Oligotrophic grassland, forest edges	9
<i>Hypomma bituberculatum</i>	Reed swamp, saline grassland	9
<i>Leptorhoptrum robustum</i>	Saline grassland	9
<i>Gnathonarium dentatum</i>	Reed swamp	9
<i>Clubiona subsultans</i>	Spruce plantation, pine forest	8
<i>Dendryphantes rudis</i>	Pine forest	7
<i>Tibellus maritimus</i>	Coastal dunes	8
<i>Tapinocyba praecox</i>	Coastal dunes	11
<i>Walckenaeria alticeps</i>	Forest edges	9

grasslands such as the sandy heaths of Breckland in East Anglia. It is widespread on the coastal dunes of Belgium (HUBLÉ & MAELFAIT 1982) and the Netherlands (NOORDAM 1993). In Sweden it occurs on the stony limestone plains of Gotland and Öland and other dry, sunny and stony habitats (Kronstedt pers. com.). In France it is widely distributed in dry heathland and calcicolous grassland, reaching 890 m in the Pyrénées (SIMON 1932, DENIS 1964, Ledoux pers. com.). In Italy (Lombardy) at 670 m it was common in xerobrometum grassland (PANTINI 2000). In Austria it has been recorded in xerothermic *Pinus sylvestris*/*Erica carnea* woodland, agricultural land, field margins and hedgerows (THALER 1997, Thaler pers. com.). Similar habitats have been recorded in Germany, together with vineyards, and shell limestone with sparse vegetation (Staudt & Blick pers. com., BAUCHHENS 1992). In the Czech Republic (BUCHAR & RŮŽIČKA 2002) it occurs in rock and forest steppes.

Most of the habitats listed have characteristics of openness, dryness and warmth with sparse vegetation and much bare ground. BUCHAR & RŮŽIČKA (2002) described the habitat of *A. cuprea* in the Czech Republic as 'Stratum: ground level, Humidity: very dry, dry, semi-humid, Light: open, partly shaded'. The graph for this species in HÄNGGI et al. (1995) has four peaks of abundance, of which approximately 47% of records were from different types of grasslands, 17% from forest edges, 20% from heathlands and vineyards, and only 9% from coastal sand dunes. In Britain *A. cuprea* tolerates a limited range of habitats but further south and east in Europe it finds suitable niches in many other situations.

Agroeca lusatica is rare in Britain and only known from a few coastal dunes in the extreme southeast. GRIMM (1986) describes this species as mainly found in eastern Europe, so the description of its preferred habitat may be close to that in BUCHAR & RŮŽIČKA (2002) 'among detritus and under stones in rock steppes, Stratum: ground, Humidity: very dry, dry, Light: open' and characteristic of thermophilous vegetation. The habitat description in GRIMM (1986) is similar. However, further west this does not always apply because RANSY et al. (1988) record it in *Calluna* heath in Belgium, LEDOUX (2001) took it in the Rhone Valley in France, Thaler (pers. com.) recorded it in bottomland forest by the River Danube, and PALMGREN (1972) found

it in a *Myrica* / *Molinia* bog in south Finland. This species is rather rare in Europe and more data are needed on its habitat ecology and perhaps of its systematics.

In contrast to *A. lusatica*, *Agroeca inopina* has a western distribution in Europe. It appears to be confined to Britain, the Channel Islands, Belgium, France including Corsica, Spain, Portugal, and Algeria (North Africa). Other published records in central and eastern Europe have been shown to be misidentifications, or cannot be confirmed because specimens cannot be traced. In Britain *A. inopina* is not uncommon in some coastal dunes and dry grassland inland. In France, similar dry, open habitats are recorded (DENIS 1964, Ledoux pers. com.). In Spain (Huesca) at 750 m – 1200 m altitude, URONES (1985) found it well-established in silver fir (*Abies alba*) forest, in *Genista scoparius* heathland, sheep folds, and oak (*Quercus* sp.) groves. In Algeria BOSMANS (1999) recorded it in eight different locations in mountain forests between 800 m and 1850 m altitude. In the north of its range it occurs in dry open areas warmed by the sun while in the south where the climate is hotter it requires some shade, but the essential features of its preferred niche are probably similar, though occurring in several different habitats.

A variant of mesotopic species are those which I have called diplostenoeicous (DUFFEY 1968) because they show a strong preference for two contrasting habitats and may be scarce elsewhere. This phenomenon was first described by BRISTOWE (1939 & 1941), although he did not give it a name. TISCHLER (1960) recorded it for an insect, and SCHAEFER & TISCHLER (1983) describe it as 'doppelter ökologisches Vorkommen'. A few examples are as follows.

Clubiona juvenis is widely associated with wetlands in many parts of Europe, especially fens and reed (*Phragmites*) swamp, and sometimes in brackish environments (SIMON 1932, PÜHRINGER 1975, DECLEER & BOSMANS 1989, HARVEY et al. 2002). It also occurs in marram (*Ammophila arenaria*) tussocks on sand dunes on the east coast of Ireland (LOCKET & MILLIDGE 1951), where I have taken it, and on the German Baltic coast (BOCHMANN 1941), where it was common on mobile and fixed dunes. Two salticids, *Marpissa nivoyi* and *Synageles venator*, also show these characteristics. The former is frequent on coastal dunes

in southern England but is also occasionally taken in wetlands. In France DENIS (1951, 1962, 1964) recorded it several times on the Vendée dunes at Longeville but also in the Camargue wetlands and in a freshwater marsh by the estuary of the Gironde. SIMON (1937) records it only from marshes and wet woodlands in France. BUCHAR & RŮŽIČKA (2002) found it on dry rock steppes 'among grass on xerothermic slopes'. *Synageles venator* is frequent on some dune systems in southern England and south Wales but is also found in extensive fen areas. SIMON (1937) records it from sand dunes but also tree trunks and hedges in France. Similarly DENIS (1943, 1961) took it in the Pyrénées-Orientales in a 'fissure des Gorges de Mordoni' and in the 'forêt de Matemale', though the habitat is not described. BUCHAR & RŮŽIČKA (2002) say it is common in both wetlands and dry rock steppes in the Czech Republic. In south Finland (PALMGREN 1972) found it in *Eriophorum* and *Myrica* / *Molinia* bogs and on coastal dunes, as did PERTTULA (1984).

Much further east in Russia and Kazakhstan *S. venator* is found in a much greater variety of habitats. In that area it appears to be eurytopic rather than mesotopic. Logunov (pers. com.) records floodplain meadows, mountain steppes, birch forests, alpine meadows, sandy areas, mountain tundra, houses, open ground, river valley meadows and swamps.

Summarising present evidence, *S. venator* seems to be diplostenocious in the northwest part of its range (Great Britain), but becomes mesotopic through central Europe and eurytopic much further east in Russia and Kazakhstan.

The habitat of *Hypomma bituberculatum* in Britain is described as 'wet swampy areas at the sides of rivers and ponds' (HARVEY et al. 2002) but it

has also been recorded as abundant on the coastal dunes of southeast Scotland (MACKIE 1971) and on the East Anglian coast of England (DUFFEY 1974). In Belgium most of the records are from wetlands and coastal dunes but it has also been taken in heathland and woodland (BAERT 1996). BUCHAR & RŮŽIČKA (2002) record it only from 'pond margins, overhanging sedge tussocks in littoral stands' in the Czech Republic. The graph for this widespread species in HÁNGGI et al. (1995) shows two high peaks of abundance and frequency for wetlands and coastal dunes, although there are records for other habitats as well.

Tibellus maritimus shows diplostenocious tendencies in Britain, although this is less clear on the European continent. In most of southern England and Wales *T. maritimus* is the characteristic species of this genus on coastal sand dunes but it is also established, but not so numerous, in wetlands further inland. *T. oblongus* is common and widespread on field-layer habitats throughout Britain. On the coastal dunes of Tentsmuir in southeast Scotland *T. maritimus* is largely replaced by *T. oblongus* (Tab. 2) (DUFFEY 1968). ALMQUIST (1973) found only *T. oblongus* on Swedish south-coast dunes, and in Finland KOPONEN (2002) and PERTTULA (1984) recorded *T. oblongus* on the main dune system and *T. maritimus* only in the dune meadow. Further south on the Dutch and Belgian coasts *T. maritimus* is the more common species on dune systems (NOORDAM 1993). However, although apparently fading away from coastal dunes with increasing latitude, *T. maritimus* occurs much further north in Europe on inland formations such as birch forest tundra (*Betula tortuosa*) in northern Finland (KOPONEN 1976) and northern Norway (HAUGE 1989).

Tab. 2. Numbers of *Tibellus maritimus* and *T. oblongus* taken on coastal sand dunes at Whiteford, South Wales, and Tentsmuir, SE Scotland. The figures have been converted to a mean of 19 hours collecting in each dune habitat. NDS: no dune slacks. Data from DUFFEY (1968).

	Drift line	Fore dunes	Yellow dunes	Marram transition	Dune heath	Dune slack	Dune meadow	Totals
Whitford								
<i>T. maritimus</i>	–	14,6	12,4	2,3	2,0	1,0	23,8	56,1
<i>T. oblongus</i>	–	1,3	–	–	–	–	–	1,3
Tentsmuir								
<i>T. maritimus</i>	–	–	–	–	2,0	NDS	–	2,0
<i>T. oblongus</i>	2,0	9,4	30,4	16,6	3,9	NDS	2,8	65,1

BRISTOWE (1939 & 1941) suggested that there is a link between these two contrasting habitats. He claimed that the interior of dense *Ammophila arenaria* tussocks 'where most spiders live, is always humid' though he did not provide measurements. This explanation has been repeated by other authors but a comparison of humidity levels between fen and dune vegetation, including seasonal variation, has not yet been made. The vegetation structure of dunes and fens is very different and we need to know how diplostenoeicous species utilise these formations, especially the development of the immature stages. Competition with associated species in these two habitats may also be important to study before we begin to understand how diplostenoeicism evolved.

Eurytopic species

By definition these species are recorded from a broad range of different major and minor habitats throughout their European range. Consequently they are usually widely distributed and common though not necessarily everywhere. In small regional areas they may show narrower habitat preferences depending on the type of landscape. They are of particular interest to the ecological arachnologist who has yet to investigate why they are so successful.

In Tab. 3 twenty species are listed as examples of eurytopism from the graphs of HÄNGGI et al. (1995). All have been recorded in 18, or all, of the 19 major habitats and in more than 60 of the 85 minor habitats. Very few eurytopic species have been investigated for habitat preferences over a wide geographical area. An exception is *Erigone promiscua*, which has a westerly distribution in Europe from the Faroe Islands to Morocco but is not yet known east of France/Belgium and the islands off southwest Norway (DUFFEY 2004). Records have been claimed for countries further east but have so far proved to be invalid or unsafe. It has been recorded in almost all habitats from very wet to very dry and from coastal dunes to inland heaths, wetlands, grasslands, agricultural land, woodland and mountains to 3600 m. Although widespread and able to establish populations in many different habitats it is not common everywhere. In the south of England it is frequent on heathlands, both wet and dry, and some grasslands but is seldom found on the coast. On the other hand on the Hebridean Islands of northwest Scotland in 1976 it was the most

abundant linyphiid on the coastal machair dunes, completely dominating the fauna (ANON. 1979).

In Britain 542 habitat records for *E. promiscua* were submitted to the Spider Recording Scheme of the British Arachnological Society for the Provisional Atlas of British Spiders (HARVEY et al. 2002). Of these 70% were recorded in dune/saltmarsh, heaths/moorland, grasslands, cultivated land/gardens, so there is a preference for open, unshaded, or partly shaded, ground habitats. Although this suggests some of the characteristics of pioneer species, *E. promiscua* is clearly eurytopic and very tolerant of a wide diversity of habitats. Pioneer species are usually defined as those which are the first to colonise newly created open ground such as agricultural land, but *E. promiscua* is not specially noted for this, although it has been recorded as common in some open situations. Many of the common pioneer species such as *Lepthyphantes tenuis*, *Meioneta rurestris*, *Erigone dentipalpis* and *E. atra* occur in numerous other habitats and are

Tab. 3. Twenty eurytopic species from the graphs in HÄNGGI et al. (1995). All were recorded in 18, or all, of the 19 major habitats and in 60 or more of the 85 minor habitats

Species	Occurrence in:		Total records
	Major habitats	Minor habitats	
<i>Alopecosa pulverulenta</i>	18/19	66/85	361
<i>Bathypantes gracilis</i>	19/19	79/85	520
<i>Centromerita bicolor</i>	18/19	63/85	234
<i>Centromerus sylvaticus</i>	19/19	76/85	467
<i>Ceratinella brevis</i>	18/19	62/85	239
<i>Cicurina cicur</i>	18/19	61/85	247
<i>Diplocephalus latifrons</i>	19/19	60/85	329
<i>Diplostyla concolor</i>	19/19	69/85	450
<i>Erigone atra</i>	19/19	77/85	632
<i>Erigone dentipalpis</i>	19/19	73/85	437
<i>Lepthyphantes menzei</i>	19/19	65/85	337
<i>Lepthyphantes tenuis</i>	19/19	69/85	431
<i>Meioneta rurestris</i>	19/19	76/85	406
<i>Micrargus herbigradus</i>	19/19	76/85	463
<i>Pachygnatha degeeri</i>	18/19	69/85	454
<i>Pardosa pullata</i>	18/19	66/85	372
<i>Robertus lividus</i>	19/19	70/85	422
<i>Trochosa terricola</i>	18/19	75/85	530
<i>Xysticus cristatus</i>	18/19	67/85	360
<i>Walckenaeria antica</i>	19/19	60/85	245

therefore classified as eurytopic. As good aeronauts their success includes the ability to be among the first colonists of new ground, whether natural or man-made.

Conclusions

Numerous publications on spider faunas in Europe seem to assume that each species has a definitive and characteristic habitat throughout its distribution. This may be because most ecological studies are often made in very limited areas where habitat differences between spiders are clearly obvious. However, on a European basis, when habitat preferences from many different localities are compared, the differences are blurred because habitat tolerance varies from place to place even within a single country. The reasons are not always clear but examples are described of species recorded from a range of different habitats but in which the same or similar microhabitats with characteristic niches seem to exist. These features appear to be more obvious in species which have a relatively limited tolerance of habitat diversity. It is possible that this phenomenon is present, in some form, in all species but only detailed studies of stenotopic, mesotopic and eurytopic spiders can reveal whether this is true.

The need for more precise and accurate descriptions of spider habitats is evident from the inadequate quality of much published data on faunal surveys. Habitat descriptions are usually based on the dominant plants associated with the major or minor habitats being studied but more information is needed if the relevant parameters required for survival and successful reproduction can be identified. Conventional habitat classification schemes are not appropriate. ELTON & MILLER (1954) and ELTON (1966) devised a system of habitat structural units which avoided botanical descriptions. However, each unit can be given a 'qualifier code' which could describe botanical, microclimatic or any other feature of ecological significance. MATVEINEN-HUJU (2004), working in Finland, used two levels of light intensity and three levels of moisture based on botanical or abiotic descriptions, but this is too limiting for general use. Perhaps the most satisfactory habitat classification so far devised is that of BUCHAR & RŮŽIČKA (2002). They describe seven levels of stratum based on structural units from below

ground to the tree canopy, as was used by ELTON (1966). This is followed by five humidity levels from very dry to very humid (marshy) and five levels of light intensity, which describe openness or shadiness of each structural unit. The assessments of the terms used in this scheme are made subjectively with the problem that if used in other countries different meanings might be applied to them. For example, the term 'very dry' may be given a different meaning in northwest Europe compared with a Mediterranean country. Nevertheless the main components of the BUCHAR & RŮŽIČKA (2002) classification can be accurately measured by available scientific instruments, for example light intensity, humidity and dryness, to which we can also add temperature. This would have the great advantage of uniformity if adopted for all ecological surveys of spider faunas.

ELTON (1966) refers to 'mounting slag-heaps of information' in publications on zoological surveys which are difficult to analyse and apply to wider ecological studies because there is no uniformity of method when recording habitats. The same situation is developing in arachnological survey literature. Future authors should bear in mind that their work would be of much greater international interest if there was agreement on trapping methods and habitat classification.

Studies of spider populations in major or minor habitats usually show that there are a few relatively abundant species and many more which are uncommon or rare. All contribute to the ecology and character of the population but statistical analysis demands high numbers so that the rarer species are rejected. This introduces a bias into the results. For example, HÄNGGI *et al.* (1995) were only able to prepare graphs for those species for which 25 literature records were available, so that most are for eurytopic species and very few for stenotopic. The bias in field work, and the number of publications in which poor ecology is camouflaged by advanced statistics, could be reduced by more extensive sampling using several different trapping techniques and by continuing the surveys for much longer periods so that more specimens are taken of the less common species. RIECKEN (1999) has shown that duration of sampling is more important than number of traps and DUFFEY (2003) that timed hand-collecting in relation to defined minor habitats was more efficient than pitfall trapping.

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