Spider habitat classification and the development of habitat profiles

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Summary

The definition of the habitat characteristics of spider species is an essential part of arachnid ecology. In this paper the method of developing habitat profiles from histograms of the number of records of occurrence for each habitat category (Hänggi *et al.*, 1995) has been followed. Those authors used published records from a wide range of sources, mainly in central Europe but also elsewhere. This paper argues that clearer and more precise profiles could be obtained by using data from each individual country so that comparisons of habitat preferences can be made between different geographical regions. The abundant data in the Spider Recording Scheme of the British Arachnological Society (Harvey *et al.*, 2002) make this possible for Britain, but it is not known whether the same amount of information is available in other European countries. An investigation of the latitudinal differences in habitat preferences in Britain was made by dividing the country into three regions: South England, North England and Scotland. A 21-category habitat classification was designed to represent the British landscape. Habitat profiles were prepared for several species in each of the three areas. In most cases habitat differences were recorded. Interpretation of these differences and the possible errors which have to be taken into account are discussed.

To do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put in a map.

Robert H. MacArthur (1984)

Introduction

The importance of habitats, their study, description and classification, attracted the attention of biologists after the establishment of the Nature Conservancy in 1949 and the creation of National Nature Reserves. Later County Wildlife Trusts also became interested as they designated their own nature reserves. The object was to assess the diversity of habitats in protected areas and the need, for conservation purposes, to identify those associated with vulnerable species of animals and plants. Numerous classification systems were proposed but none achieved general acceptance because of differing opinions on how to represent the complexity of the British landscape.

The main problems in the early years were:

1. The belief that a habitat classification should include all animal and plant groups.

2. The large numbers of habitat categories thought to be relevant were not of equal importance. How does one choose?

3. The failure to define each category so that it was clear what to include or exclude.

4. The attempt to find a workable habitat classification applicable to a large area such as the whole of Europe.

Habitat classifications are only workable if designed for a particular wildlife group. A design for vertebrates is not suitable for invertebrates or plants. The classification proposed here is for medium-sized invertebrates such as arachnids and possibly some insect groups, and has the construction of habitat profiles as its primary objective. The habitat categories selected should be of approximately equal ecological importance and, although this must be a subjective assessment, the problem is easier to resolve if the classification is designed for one or more related wildlife groups. This also simplifies the definition of habitat categories. The "ecological importance" of the chosen habitat categories is assessed based on a variety of factors, some of which may not necessarily apply in all cases. Area and a wide distribution are important, as is knowledge of the British fauna. Permanence of a habitat for a long period, such as in the case of some fens, forests, heaths, sand dunes and saltmarshes, is also relevant. Other habitat criteria of importance are those difficult to modify by man or which are of no agricultural use, such as rocks, screes, cliffs and mountain tops. Some habitat categories are important only because they cover very extensive areas, notably agricultural land, buildings and industrial regions.

Habitat classifications which attempt to cover large areas with increasingly complex landscapes may have problems of interpretation because most animals which are widespread modify their habitat preferences according to geographical region (Duffey, 2005). Consequently, profiles based on large areas contain so many variables of habitat tolerance that no clear preferences may be revealed.

The nomenclature in this paper follows Russell-Smith (2008).

Material and methods

Habitat classification for spiders

The habitat classification of Hänggi *et al.* (1995) was designed specifically for spiders and has 19 major land-form categories subdivided into 85 minor habitats. Where the data were sufficient the authors were the first to construct histograms as species habitat profiles, and I have followed this system. They used only published records and required a minimum of 25 to be able to compile a species histogram. However, some of their profiles did not give clear examples of habitat preferences, partly because they included records from a wide range of different European countries and partly because most species with sufficient data were eurytopic or mesotopic, i.e. very habitat-tolerant and able to adapt to numerous different habitat categories. Few of the rarer and more habitat-specific stenotopic species could be included because there were too few records. Nevertheless, Hänggi *et al.* (1995) were able to include some interesting examples.

Category	Definition
1. Saltmarsh, foreshore driftlines and shingle banks reached by the tide.	All coastal.
2. Sand dunes	All coastal. Embryo dunes to dune meadow. Includes Scottish machair.
3. Coastal rock shores and cliffs	All coastal: reached by tide or salt spray. Grassland at top of a cliff or inland from a rocky shore is classified as terrestrial not coastal.
4. Grasslands, calcareous	On calcareous soils, chalk or limestone. Semi-natural grassland but may be grazed.
5. Grasslands, neutral	Semi-natural grasslands not clearly acidic or calcareous. Covers some upland sheep-grazed areas and valley meadows. Not to be confused with sown or "improved" grasslands which are often on neutral soils and should be included in "Cultivated land".
6. Grasslands, acidic	Acidic semi-natural grasslands on poor sands and gravels (not coastal) and other leached soils.
7. Heathland	Vegetation of ericaceous plants, mainly *Calluna* and *Erica* spp. and fine-leaved grasses. Mostly dry acidic soils but may include temporary wet areas. Heavy grazing by rabbits or sheep may convert heath to mainly grass.
8. Woodland, broadleaf	Includes all species of broadleaf trees — canopy, trunks, bushes and ground vegetation. Includes very small glades surrounded by trees.
9. Woodland, coniferous	Mainly plantations, young and old. Some natural pine forest in Scotland.
10. Woodland, mixed	See text. Semi-natural coniferous broadleaf mixtures are very rare. Man-made mixtures, broadleaf with coniferous nurse crop, are infrequent. Where conifers and broadleaf trees are adjacent but separate use categories 8 and 9.
11. Scrub	All types (outside woodlands) including gorse and hedgerows.
12. Marsh	Wetlands, often linear, bordering larger rivers, lakes and reservoirs.
13. Fens	Vegetation clearly not acidic. Usually water-fed by springs, ditches, dykes or streams. Including reed and *Cladium* beds.
14. Peat bogs, moorland	Wet acidic peatlands usually with ericaceous plants and *Sphagnum* mosses. Includes blanket bog and upland moorland on peat soils.
15. Rocky areas, screes, shingle banks	All inland. Mainly in upland areas. Includes shingle banks by rivers and streams. Also limestone pavements.
16. Mountains	Rock or vegetated areas at, or over, 2000 ft (615 m).
17. Caves, mines and culverts	Natural or man-made. Places where light is excluded. Some species, not normally found in dark places, may sometimes occur, e.g. in sewage filter beds. These should be allocated to category 20.
18. Cultivated land	Arable with or without crops, market gardens, agricultural grasslands (sown leys and "improved" grassland). Football pitches and playing fields.
19. Gardens and parks	Private and public; includes arboreta and glasshouses in botanic gardens.
20. Buildings	Private and industrial; offices; urban areas. Includes isolated buildings if occupied or used. Isolated unoccupied huts, sheds and temporary structures should not be included but assigned to the habitat around them.
21. Industrial land	Used or abandoned. Industrial wasteland. Quarries, spoil heaps, bare ground of opencast mining, railways, road surfaces and car parks.

Table 1:   Spider habitat classification with 21 categories.

The habitat classification system which the British Arachnological Society has used for its Spider Recording Scheme (SRS) originally had 23 categories between 1987 and 2002, but after the publication of the Provisional Atlas (Harvey *et al.*, 2002) other categories were added. The need for continuity with previous data meant that the opportunity to redesign the classification was limited and the old categories were retained, resulting in a total of 36. This means that some categories lack clarity or appear ambiguous. In order to avoid these problems I have, for the purpose of this paper, reduced the total of categories to 21, including one not in the SRS system. Each one is defined to make clear the landscape forms which are included, as well as their limitations and exclusions (Table 1). Category 3 (Coastal rock shores and cliffs) is not included in the results as it was not represented in the SRS system.

Every habitat classification is a compromise because of the infinite complexity of the (British in this case) landscape, which has to be simplified to a smaller number of meaningful ecological units. The wider the geographical area covered by the classification the more difficult is the choice of habitat categories. For this reason it is probably better for each country to devise its own classification system, as this will indicate more clearly the change in habitat tolerance of each species from one geographical area to another. The definition of habitat categories in Table 1 is intended to include only the ecologically significant features relevant to spiders, but can no doubt be improved with use and experience. As the definitions are rather brief it is necessary to offer further explanation and discussion, as follows.

Grasslands

The division between man-made and semi-natural grasslands is important because habitat permanence is essential for some of the more specialised spider species.

It would seem more appropriate to classify grasslands in terms of structure, density and height, which determine where most spiders live, rather than by soil type (calcareous, neutral, acidic). Soil alkalinity or acidity has a strong influence on the grass sward but does it also influence the spider fauna? Edwards *et al.* (1975) studied the spider fauna of the ancient grass plots at the Rothamsted Experimental Station. These were established in 1856 in permanent semi-natural grasslands to test the yield differences between plots having various manure treatments. In the early 20th century some of the plots were treated either with organic manure, mineral fertilisers, nitrogenous fertilisers or mixtures with different quantities of nitrogen. During the study of the spider fauna in 1973/74 the soil pH varied after treatment from 3.8 to 7.5 according to plot. Spiders were collected in 392 pitfall traps operated for 1 day in each month of a 12-month period. In spite of the wide difference in pH values the authors concluded that soil characteristics had "little direct effect on the number of spiders" and that "differences in the spider population of the plots were most likely caused by differences in plant diversity, density and height". In spite of the problem of using soil types for the grassland divisions, the terms calcareous, neutral and acidic are usually easily recognised in the field and no suitable terms describing grassland density and structure have been found.

Woodlands

The categories Broadleaf and Coniferous are self-evident but "Mixed woodland", which implies that both types may be equally represented in some forest areas, requires further examination. Coniferous and broad-leaved trees growing together is a rare and specialised habitat in the small area of semi-natural woodland still surviving in Britain. The distinguished forest ecologist Dr George Peterken (pers. comm.) advises me that there are a few examples of beech/yew (*Fagus/Taxus*) associations on chalk soils in the south of England and birch/pine (*Betula/Pinus*) on northern limestones. In Scotland there are a few holly/yew (*Ilex/Taxus*) and birch/pine mixtures and some remnants of oak/pine/birch (*Quercus/Pinus/Betula*) still survive. These rare specialised habitats in Britain may not be visited very often by the arachnological collector but he will be familiar with conifer plantations of all ages and sometimes with conifer nurse crops in broadleaf plantations. Many conifer plantations have protective margins of broadleaf trees and sometimes a wooded area is part broadleaf and part conifer, adjacent to each other but not mixed. In these cases the arachnologist has an option where to collect and to assign the material to categories 8 or 9 (Table 1) as appropriate. On the continent of Europe broadleaf/coniferous woodlands are often widespread and may be an important habitat for spiders.

Peat bogs, blanket bog and moorland

These important habitats are grouped together because all are peat-based and occur in high rainfall areas. Wet bogs with *Sphagnum* mosses are easily recognised and most common in the north of England, Wales and Scotland. Moorland is much more widespread, occurring from Cornwall to the north of Scotland, and is better represented in Britain than on the continent of Europe (Rackham, 1986). Nevertheless, we probably know more about the arachnid fauna of wet bogs than of moorland. As our information increases and if moorland is shown to have a distinct fauna, the peat habitats could be separated. The distinction between moor and heath is not always clear because both may have ericaceous plants. Rackham (1986) describes heaths as occurring in dry parts of the country on mineral soils in contrast to moorland on peat. He also comments that heaths are usually a product of human activity following woodland clearance but moors are more stable and less of an artefact.

Parks and gardens

Town parks and gardens are, in most cases, man-made but some National Trust properties and other large rural areas described as "Gardens" may include semi-natural grassland, wetland or heath as well as formal gardens. Normally there should be little difficulty in separating the formal from the semi-natural.

Inland and coastal rocky areas

The SRS habitat category "Rock, scree, cliff or quarry", which one assumes refers to inland areas, includes both natural features "rock, scree, cliff" as well as "quarry", which is man-made and when abandoned will change as vegetation develops. In the revised 21-category system "Quarry" is therefore transferred to "Industrial land".

The habitat profile

The SRS of the British Arachnological Society is able to offer many more habitat records than were available to Hänggi *et al.* (1995). For two common species, *Tenuiphantes tenuis* and *T. zimmermanni*, over 6000 habitat records are available for the former and 5200 for the latter. Consequently many eurytopic species can be adequately profiled. Somewhat fewer mesotopic species and a small number of stenotopic species can be illustrated in the same way.

The profile shows the categories of habitats most frequently associated with a species and also the degree of tolerance or intolerance of habitat diversity. Stenotopic species show the greatest intolerance as their specialisation may confine them to only one habitat category. They are often rare because their habitat tolerance is so limited, but this is not always the case in all geographical areas. The habitat may be specialised but it may not be scarce. Stenotopism is not always a fixed characteristic, e.g. *Synageles venator* and *Philodromus fallax* Sundevall (not illustrated) are stenotopic in Britain but may be mesotopic or even eurytopic further east in Europe (Duffey, 2005).
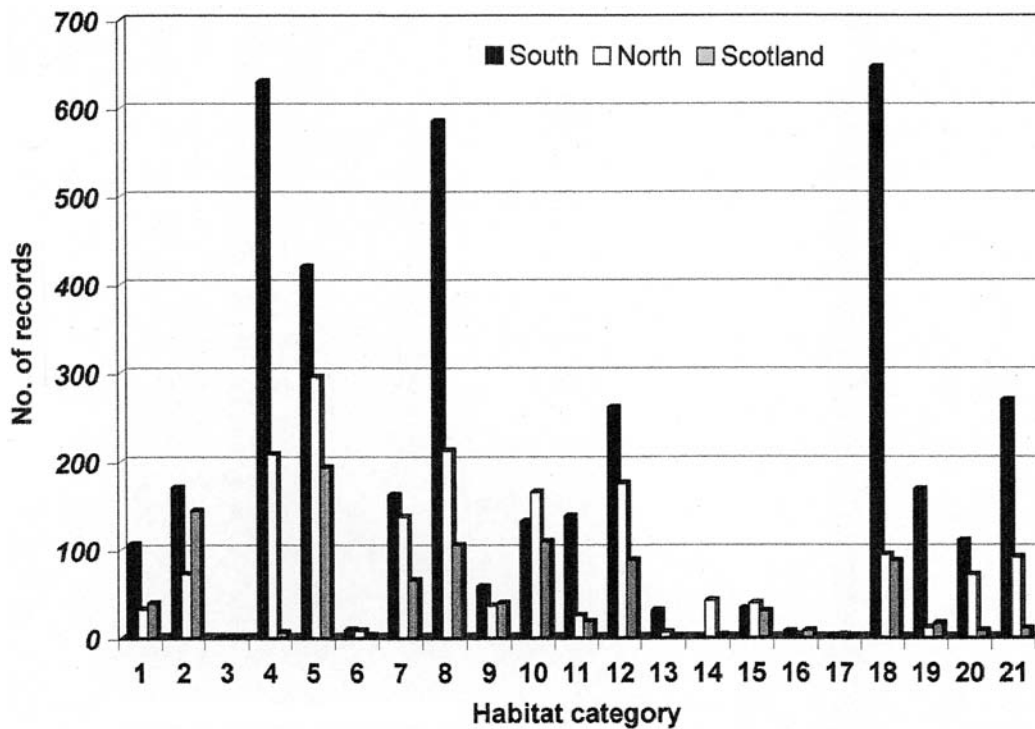
Fig. 1: Habitat profile of *Tenuiphantes tenuis* (Blackwall, 1852).

Mesotopic species show greater habitat tolerance and usually a clear peak in the profile, or more than one, and also a lesser presence in several other habitat categories, demonstrating an ability to survive in a number of different biotopes. The trend continues to the eurytopic species, which show the greatest habitat tolerance by being recorded in all or nearly all of the habitat categories in the classification system. These species are the most frequent and widespread in the British spider fauna.

The terms stenotopic, mesotopic and eurytopic are useful in classifying different types of habitat profile but they only represent stages in a cline from strict specialisation to an ability to adapt to many different habitats. Consequently there are many intermediate forms. Habitat characterisation of spider species has been represented in the arachnological literature for many years, based mainly on anecdotal data or personal experience. Generally there were insufficient records to form clear distinctions and much depended on the opinion of the collectors. The habitat profile now presents an opportunity to define habitat preferences in quantitative terms based on a large number of independently collected data held by the SRS of the British Arachnological Society. As far as I am aware no other country in Europe has operated a similar system.

The habitat profile in relation to geographical area

Although there is evidence that preferred habitats may change according to geographic location (Duffey, 2005), it is difficult to illustrate this quantitatively for different countries, with the possible exception of Britain. However, the UK may be too small to demonstrate geographic differences in habitat selection by a particular species, for example, between the northern and southern counties of England and of Scotland. Nevertheless it was decided to test this possibility for two pairs of very common species, *Tenuiphantes tenuis* and *T. zimmermanni* and *Erigone atra* and *E. dentipalpis*, because their records were so numerous in the SRS. To represent the south of England 28 vice-counties (Dandy, 1969) were selected extending from the south coast to approximately level with Oxford. In middle England, 21 vice-counties were excluded from the trial in order to provide more contrast between south and north. The latter was represented by 16 vice-counties extending from level with Manchester to the Scottish border. Scotland forms the third region, with 41 vice-counties. The exclusion of middle England to emphasise latitudinal differences leaves out the important East Anglian counties as well as the Midlands and Wales. A further study of the arachnid fauna of East Anglia, the Midlands and Wales is needed to investigate whether habitat profile differences exist from east to west.

The total numbers of records in the BAS Spider Recording Scheme for each habitat category for the 28 species used as examples in this paper are given in Appendix 1.

Results and discussion

Eurytopic species profiles

Tenuiphantes tenuis *and* T. zimmermanni (Figs. 1 and 2)

These two species are common and widespread in Britain and, as would be expected, there are obvious similarities in the profiles. Nevertheless there are also differences. *Tenuiphantes zimmermanni* demonstrates a closely packed group of peaks around Heathland,
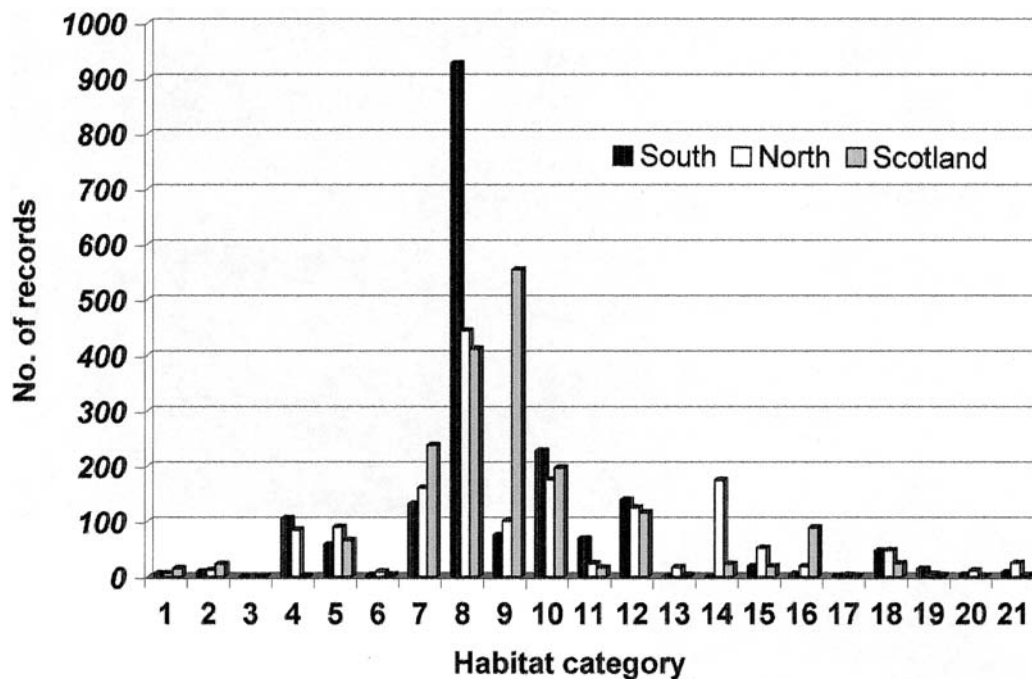
Fig. 2: Habitat profile of *Tenuiphantes zimmermanni* (Bertkau, 1890).

Broadleaf, Coniferous and Mixed woodlands (7–10) for all three regions, whereas *T. tenuis* is more widely scattered. The highest peaks for *T. tenuis* in South England are for Calcareous grassland (4), Broadleaf (8) and Cultivated land (18) and there are lesser peaks in Neutral grassland (5), Marsh (12) and Industrial land (21). The peaks for North England for categories 4, 5, 8 and 12 are similar to those in South England but smaller, while in Scotland *T. tenuis* is widespread but with few records. *Tenuiphantes zimmermanni* seems to have a clear preference for Coniferous woodland (9) in Scotland, possibly because this habitat is much more widespread than Broadleaf. The number of records in the 20 habitat categories for *T. tenuis* are South England (3937), North England (1725) and Scotland (974) and for *T. zimmermanni* South England (1855), North England (1591) and Scotland (1815). It is interesting that there are twice as many records for *T. zimmermanni* in Scotland than for *T. tenuis* and the latter is four times more numerous in South England than in Scotland. This is probably a realistic assessment of the relative numbers of these two species in the UK. On a regional basis these species may show a similar difference in numbers. Timed hand-collections in three East Anglian groups of fens, Breckland, Broads and Suffolk coast, showed that *T. tenuis* was frequent in each, scoring respectively 26, 46 and 67. On the other hand *T. zimmermanni* was abundant only in the Suffolk fens (496) in contrast to the Breckland fens (13) and the Broads (11) (see Duffey & Feest, 2009). The Hänggi *et al.* (1995) profiles based mainly on Central European data show *T. zimmermanni* with a preference for broadleaf woodland, as in South England. There are peaks in oak/hornbeam (*Quercus/Carpinus*) and beech forests and also for dwarf shrub heath. The *T. tenuis* profile is more difficult to understand as there are only two peaks, in saline grassland and coastal sand dunes.

Erigone atra *and* E. dentipalpis (Figs. 3 and 4)

The *E. atra* and *E. dentipalpis* profiles are very similar and demonstrate well-developed eurytropism. Both have a high peak in Cultivated land (18), a strong presence in several other habitats and also share few records in Acidic grassland (6), Fens (13), Peat bogs (14), Rocky scree and shingle (15), Mountains (16), Caves, mines and culverts (17). They are also more numerous in South England than in North England or Scotland, with *E. atra* generally scoring higher totals than *E. dentipalpis* except in Scotland. The only apparent difference between the two species is the much larger number of records for *E. dentipalpis* in Gardens and parks (19). Species evolve because they have developed different life histories from related populations and this usually includes different habitat preferences as well. For this reason the great similarity in distribution and habitat of these two species is surprising and it is possible that the data available may be insufficient to detect small differences. Perhaps the development of uniform man-made landscapes has brought them closer together and made differences more difficult to detect. The Hänggi *et al.* (1995) profiles for these two *Erigone* species in Central Europe are also very similar with records in 77/85 minor habitats for *E. atra* and 74/85 for *E. dentipalpis*. Both have high peaks in agricultural land (cereal crops) and saline grassland. The only difference is a secondary peak in "moist littoral areas" for *E. atra* and few records for *E. dentipalpis*. These two species clearly need more study.

Both *T. tenuiphantes* and *zimmermanni* and *E. atra* and *dentipalpis* appear to adapt to whatever is the most frequent habitat in the region where they occur. The lower scores in Scotland may be partly due to fewer recorders compared with South England but probably is a true reflection of lower populations in North England.

All four species were recorded in at least 19/20 of the habitat categories (and at least 18 in each region). No. 3
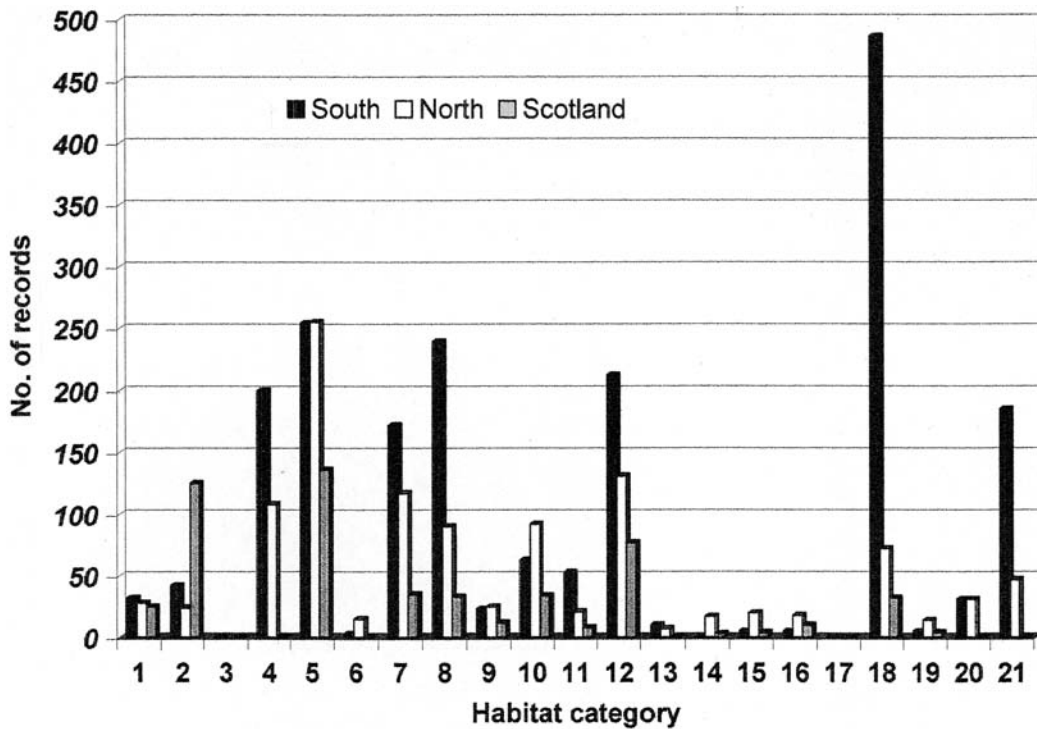
Fig. 3: Habitat profile of *Erigone atra* Blackwall, 1833.

is not included in the 21 as it was not represented in the SRS system. In the Hänggi *et al.* (1995) classification *E. atra* and *E. dentipalpis* were recorded in 77 and 73 respectively of the 85 minor habitat categories. *Tenuiphantes tenuis* was equally habitat-tolerant at 70/85 but *T. zimmermanni* scored only 43/85.

Other eurytopic species profiles

Saaristoa abnormis (Fig. 5) is clearly a northern woodland species with highest peaks in Coniferous woodland (9), Broadleaf (8) and Heathland (7), all in Scotland. It is generally less common in North England than in Scotland except for Peat bogs (14) and Calcareous grassland (4), for which there are few records for South England and none for Scotland. In Central Europe it has peaks in forest edge and dry broadleaf (Hänggi *et al.*, 1995). *Ceratinella brevipes* (Fig. 6) also has its highest number of records for Heathland (7) in Scotland, with North England close behind. There are lesser peaks in Scotland in Coniferous woodland (9), Broadleaf (8) and Marsh (12). Dwarf shrub heath, reed beds and moist
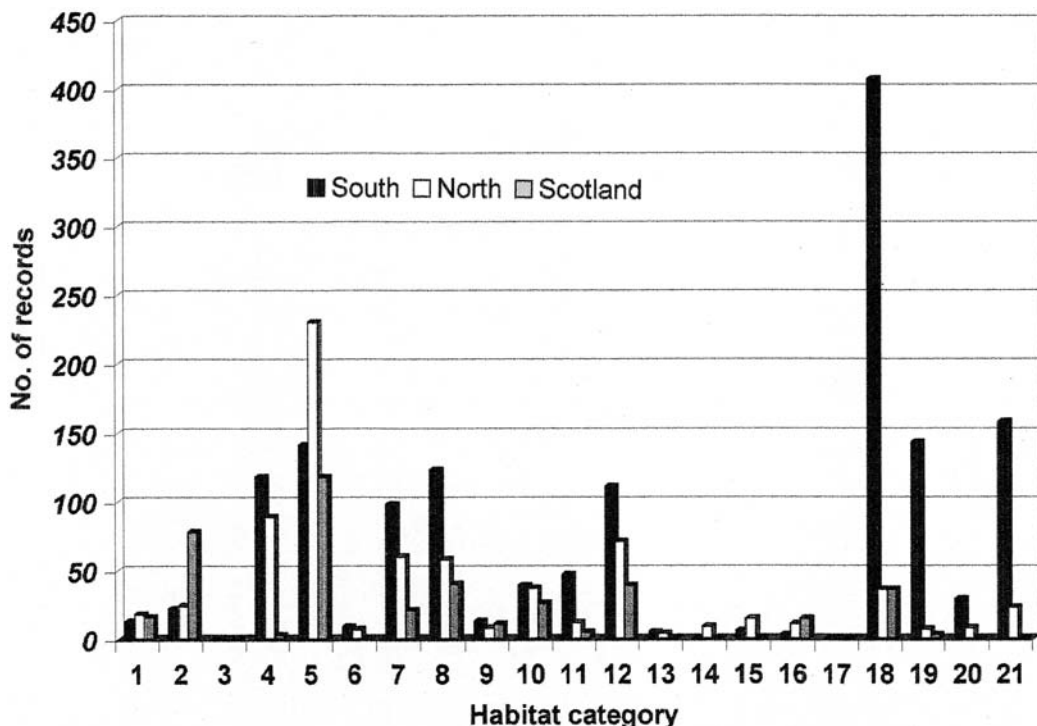

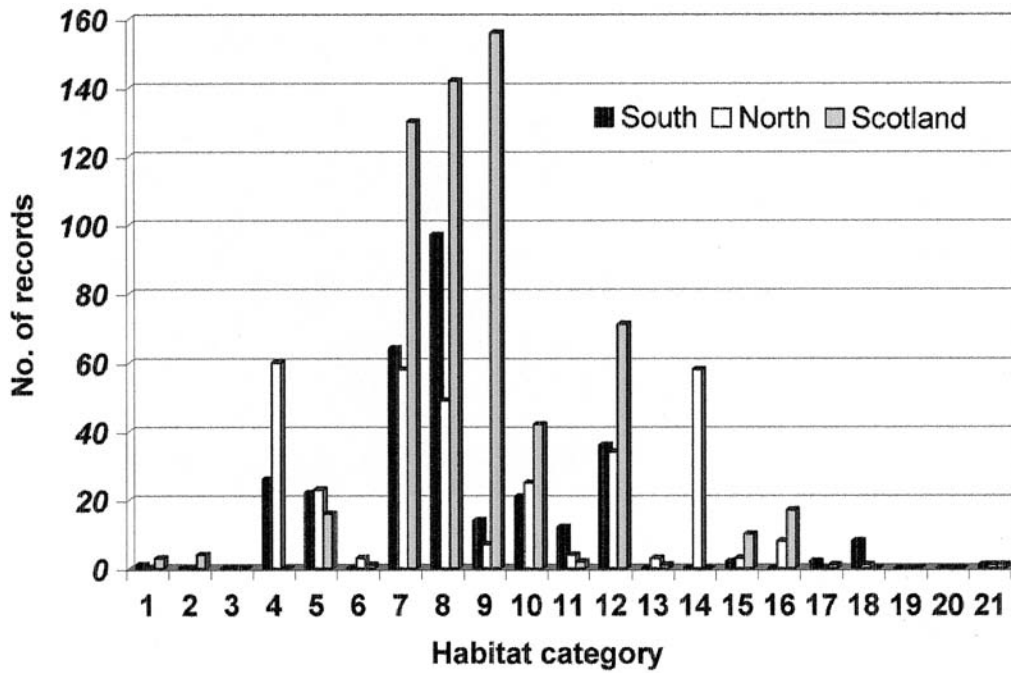Fig. 4: Habitat profile of *Erigone dentipalpis* (Wider, 1834).

Fig. 5: Habitat profile of *Saaristoa abnormis* (Blackwall, 1841).

meadows were the preferred habitats in Central Europe (Hänggi *et al.*, 1995). *Gonatium rubens* (Fig. 7) scores highly for Calcareous grassland (4) in South England but is most abundant in Scottish Heathlands (7). In North England both *C. brevipes* and *G. rubens* have their highest numbers in Heathland (7) and Peat bogs (14). *Enoplognatha ovata* (Fig. 8) is primarily a species of South England with five peaks at, or over, 150 records. *Bathyphantes gracilis* (Fig. 9) is similar, with four high peaks near, or over, 300 records in Calcareous grassland (4), Broadleaf (8), Marsh (12) and Cultivated land (18). Hänggi *et al.* (1995) have only one peak for this species

in Central Europe, in dwarf shrub heath. *Alopecosa pulverulenta* (Fig. 10) has four peaks in South England, Calcareous grassland (4), Neutral grassland (5), Cultivated (18) and Industrial land (21), and one in Scotland (Heathland), with smaller peaks in North England in Calcareous and Neutral grassland. Hänggi *et al.* (1995) record peat bogs, moist meadows, fallow grassland, acidic grassland and forest edges for Central Europe.

Centromerita bicolor (Fig. 11) records its highest peak for Cultivated land (18) in South England but there are lesser peaks for Sand dunes (2), Neutral grassland (5) and Marshes (12) in Scotland. In North England the
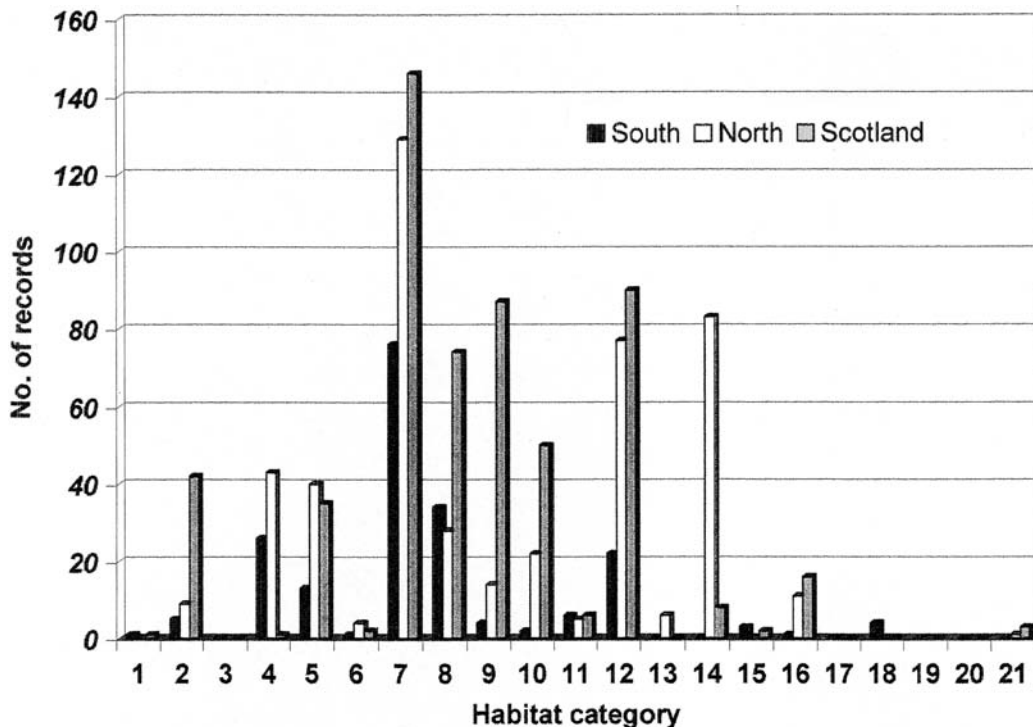

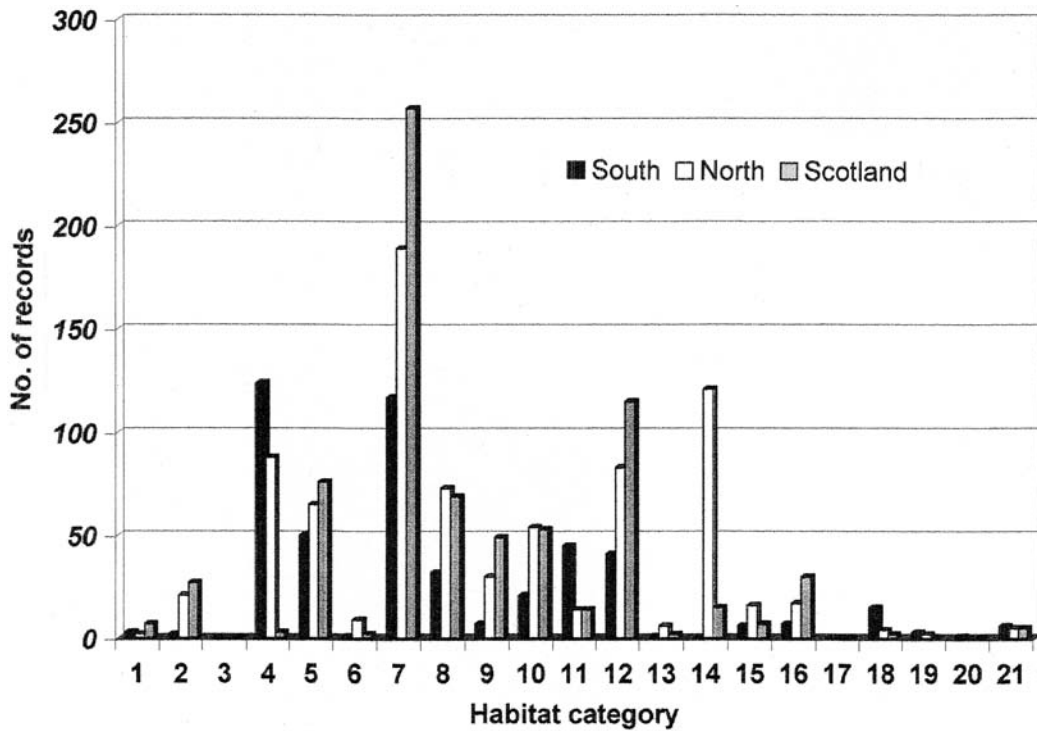Fig. 6: Habitat profile of *Ceratinella brevipes* (Westring, 1851).

Fig. 7: Habitat profile of *Gonatium rubens* (Blackwall, 1833).

highest peak is for Neutral grassland (5), closely fol-
lowed by Heathland (7). It was present in 19/20 habitat
categories. Hänggi *et al*. (1995) also record numerous
peaks for this species in Central Europe, moist grassland
and sown grasslands being the highest. It was recorded
in 58 of the 85 microhabitats.

Maso sundevalli (Fig. 12) occurred in 19/20 habitat
categories but shows a clear preference for Broadleaf (18)
in South England. In Central Europe Hänggi *et al*. (1995)
record the highest peak in coastal sand dunes and a
second peak in forest edge. There are records for 53/85

microhabitats. *Talavera aequipes* (Fig. 13) is essentially a
southern species and scores well in Calcareous grassland
(4), Neutral grassland (5) and Heathland (7), but the
highest peak is for Industrial land (21), all in South
England. It is not profiled or listed by Hänggi *et al*. (1995).

Mesotopic species profiles

Centromerus arcanus (Fig. 14) is a northern species,
with four peaks in Scotland. The highest is for Conifer-
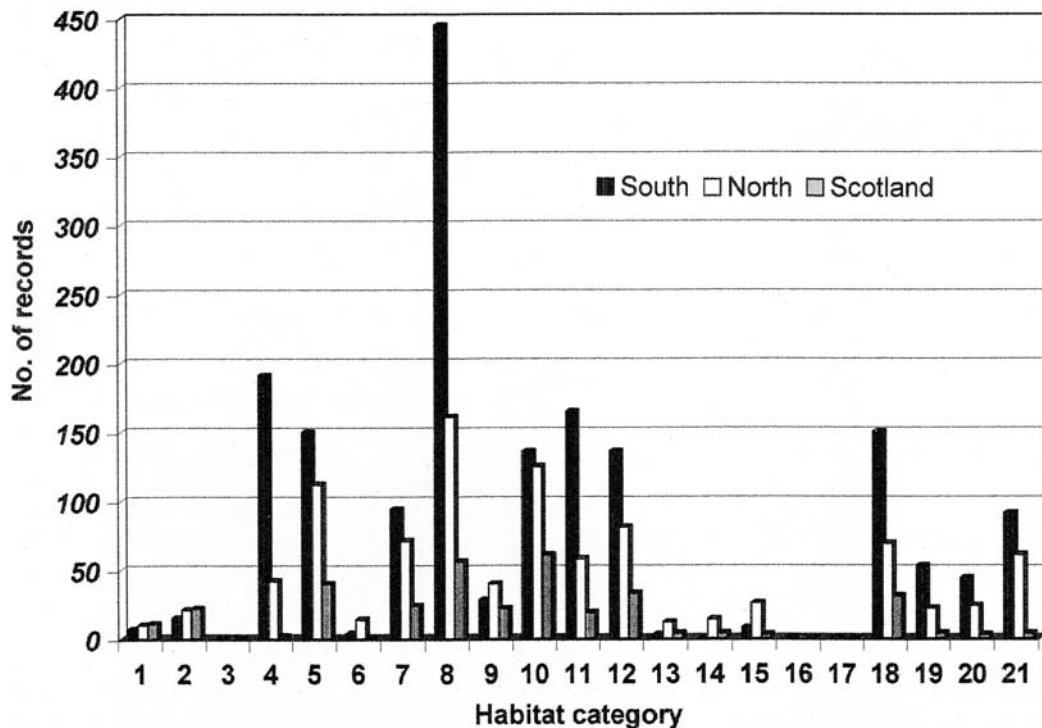ous woodland (9) followed by Mixed woodland (10),

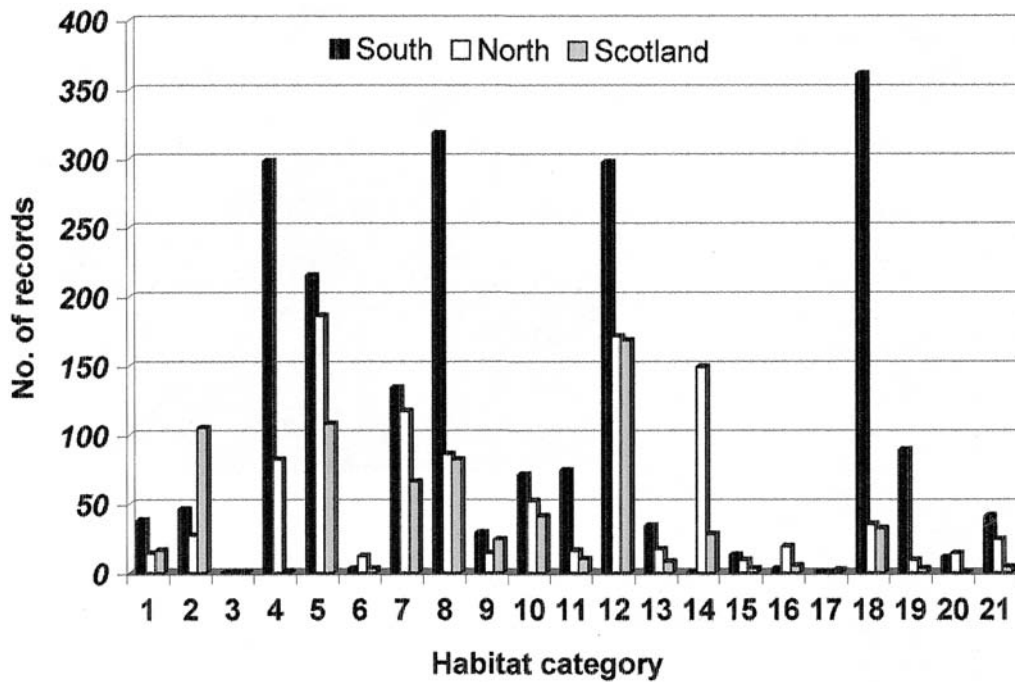Fig. 8: Habitat profile of *Enoplognatha ovata* (Clerck, 1757).

Fig. 9: Habitat profile of *Bathyphantes gracilis* (Blackwall, 1841).

Heathland (7) and Marsh (12). North England records a peak in Peat bogs (14) and lesser ones in Marsh and Coniferous woodland. *Porrhomma pallidum* (Fig. 15) is also northern, with a high peak in Coniferous woodland (9) in Scotland and much smaller ones in Broadleaf (8), Marsh (12) and Heathland (7). In North England it shows no distinction between Broadleaf and Coniferous woodland. *Hypselistes jacksoni* (Fig. 16) has its highest peak in North England Peat bogs (14) and is well represented in the Heathland (7) and Marshes (12) of all three regions. The relatively common species *Linyphia hortensis* (Fig. 17) records a strong preference for Broadleaf (8), especially in South England. In Central Europe (Hänggi *et al.*, 1995) there are peaks in oak/

hornbeam, poplar/willow (*Populus/Salix*), beech and hedges. *Xysticus kochi* (Fig. 18) is entirely southern apart from two records in North England Sand dunes (2) and one in Marsh. Most records are for Industrial land (21) followed by Neutral grassland (5) and Sand dunes (2). In Central Europe Hänggi *et al.* (1995) record the highest peak in coastal sand dunes and a subsidiary peak in industrial land, so there is little difference between the two geographical regions.

Stenotopic species profiles

These species are generally confined to specialised habitats, but some are more tolerant than others.
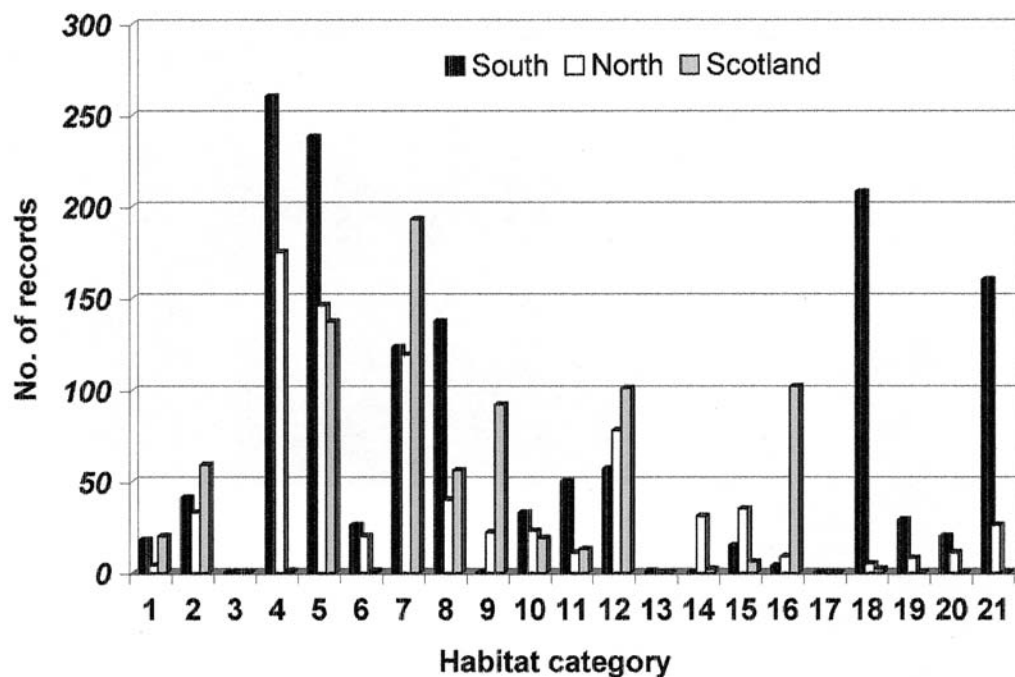

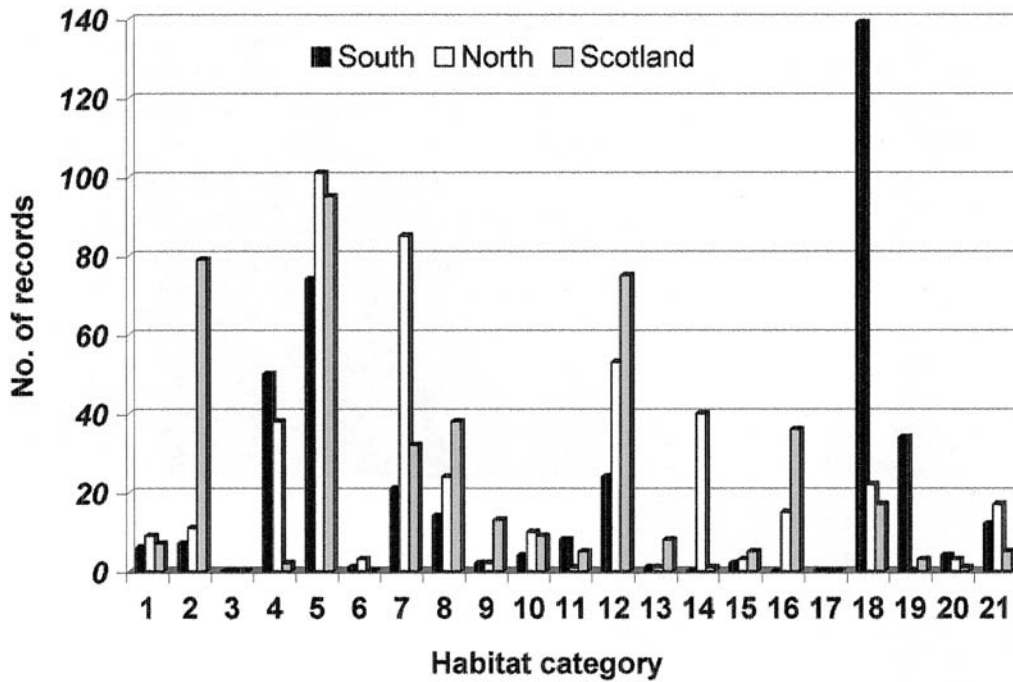Fig. 10: Habitat profile of *Alopecosa pulverulenta* (Clerck, 1757).

Fig. 11: Habitat profile of *Centromerita bicolor* (Blackwall, 1833).

Carorita paludosa Duffey (not illustrated but see Duffey & Feest, 2009) is known from only one habitat in England, where it may be locally numerous. *Sitticus saltator* (Fig. 19) and *Zodarion italicum* (Fig. 20) are almost confined to a single specific habitat in South England, while *Simitidion simile* (Fig. 21) is clearly a Heathland (7) species in South England but is also recorded from 15 other habitat categories, some in low numbers, but with good numbers in Neutral grassland (5), Scrub (11) and Industrial land (21). The profile for *S. simile* in Central Europe (Hänggi *et al.*, 1995) has only one peak, for fruit trees, but there are records for 14 other habitats. For France Le Peru (2007) lists heather,

broadleaf, juniper shrubs, marshes, holm oak (*Quercus ilex*) and heathland. During my 11 years living in France I took it fairly frequently in hay meadows, moist grassland and hedgerows. *Leptothrix hardyi* (Fig. 22) has relatively few records but has been most often recorded in Neutral grassland (5) in North England and there are records for Heathland (7) in all three regions. Two common species have stenotopic profiles, *Argyroneta aquatica* (Fig. 23) in water (Marshes — 12) and *Achaearanea tepidariorum* (Fig. 24) on Buildings (20). Although the British profile classifies *A. tepidariorum* as stenotopic, Hänggi *et al.* (1995) record oak/hornbeam woodland and alder forest, and in France
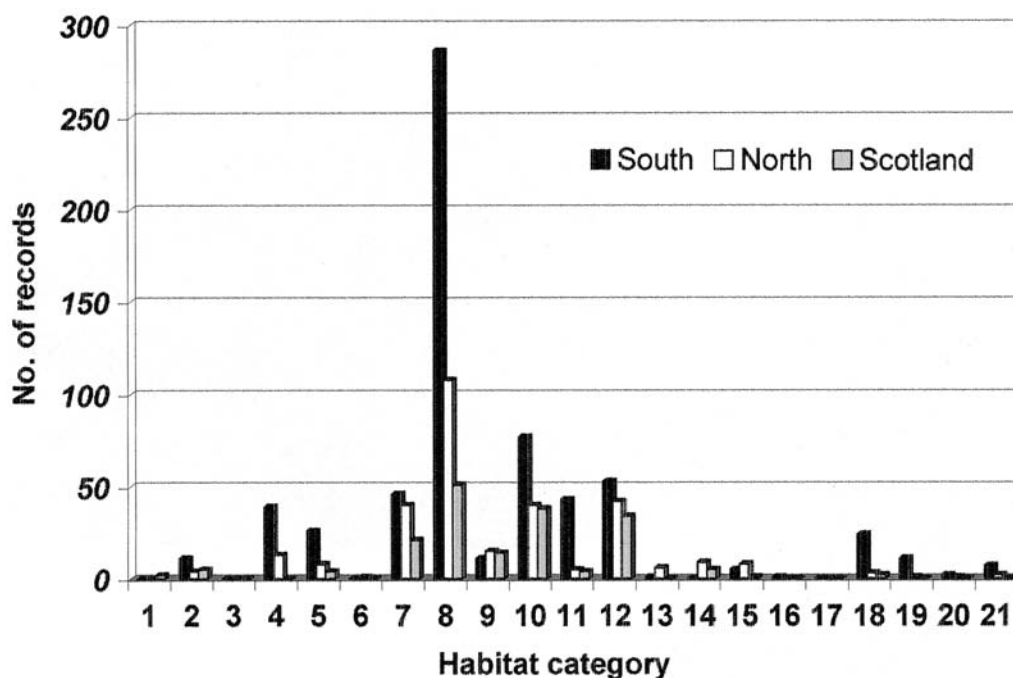

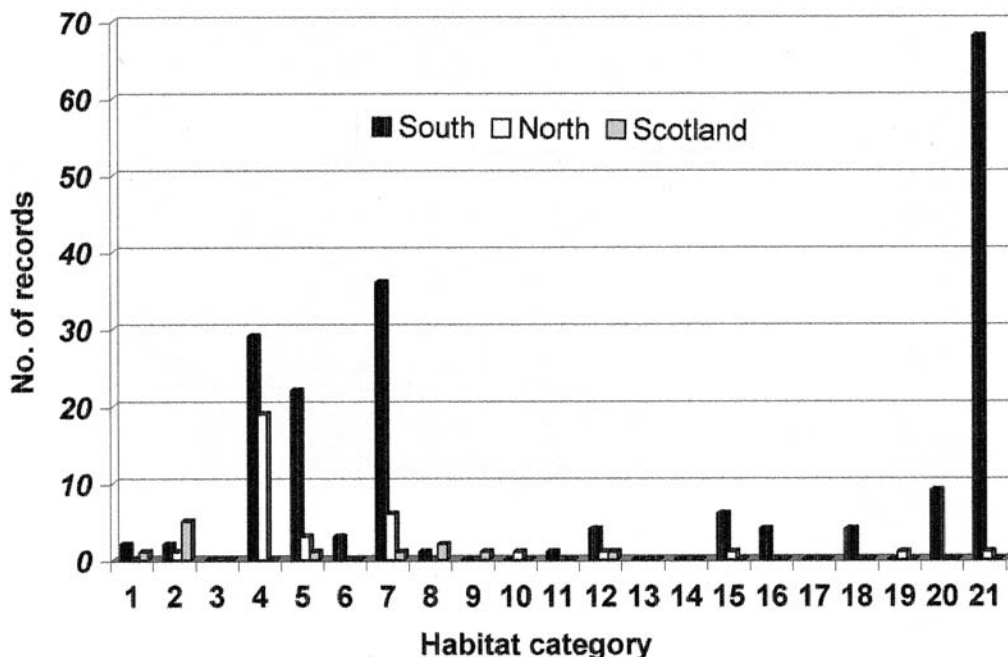Fig. 12: Habitat profile of *Maso sundevalli* (Westring, 1851).

Fig. 13: Habitat profile of *Talavera aequipes* (O. P.-Cambridge, 1871).

Le Peru (2007) quotes three records for pine forest as well as buildings. *Mangora acalypha* (Fig. 25) is a South England species found mainly on Heathland (7). The highest peak in Hänggi *et al*. (1995) for Central Europe is in potato fields, followed by cultivated land and gardens. This is in contrast to Le Peru (2007), who lists more than 23 different habitats in France, including different types of forest, grasslands, heaths, marshes and peat bogs.

The British and Central European profiles for *Zelotes electus* (Fig. 26) are very similar, as the highest peaks for both are for Coastal sand dunes (2). Nevertheless there are 9/20 other habitats recorded in Britain and 14/85 in Central Europe. *Arctosa perita* (Fig. 27) and *Diplocephalus latifrons* (Fig. 28) are intermediate between stenotopic and mesotopic. For *A. perita* the profiles for Britain and Central Europe are similar. Coastal sand dunes (2) and Industrial land (21) are the main peaks. It was recorded in 13/20 other habitats in Britain and 11/85 in Central Europe. The three highest peaks for *D. latifrons* in Britain are for Broadleaf (8) in all three regions, with the highest in South England. In Central Europe the main peak is for pine forest but there are lesser peaks for forest edge, poplar/willow woodland, beech forest and hedges. There are records for 59/85 other habitats in Central Europe and 17/20 for Britain.
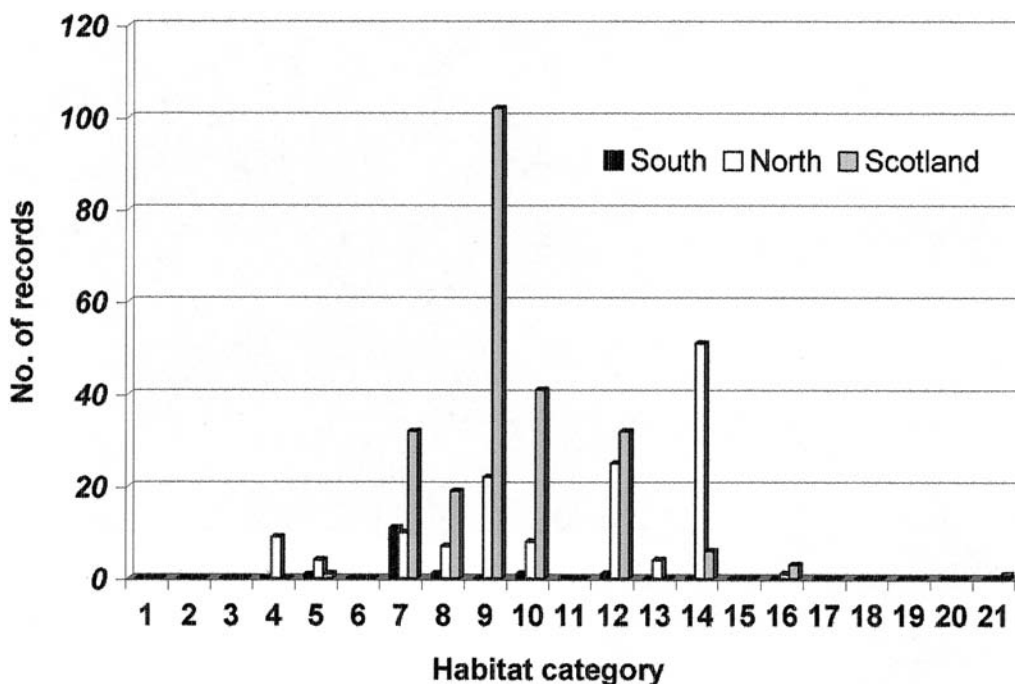

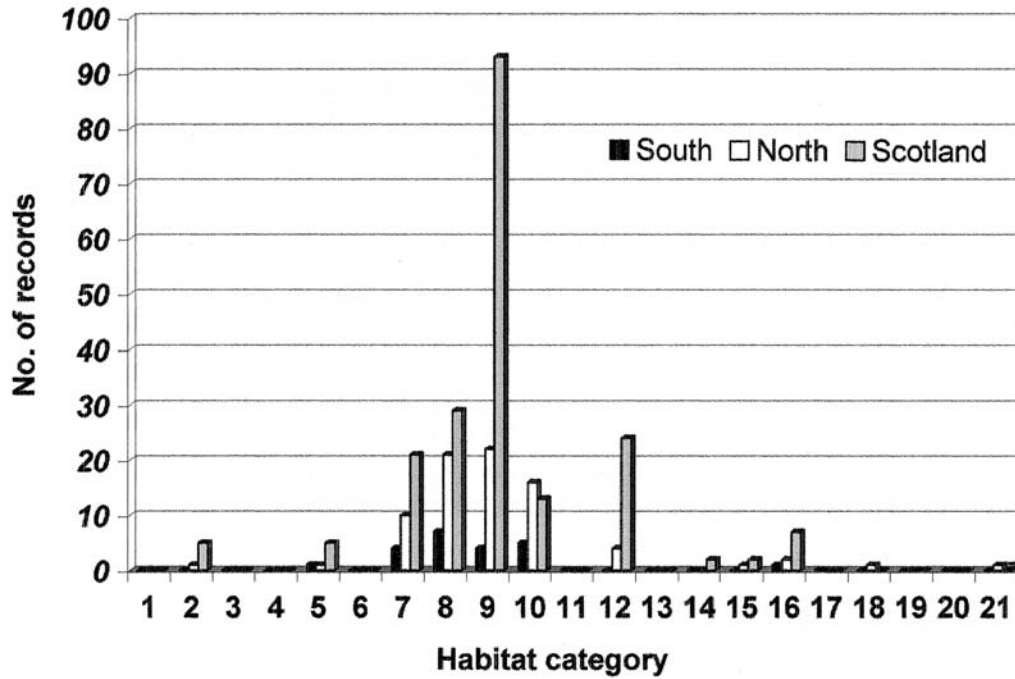Fig. 14: Habitat profile of *Centromerus arcanus* (O. P.-Cambridge, 1873).

Fig. 15: Habitat profile of *Porrhomma pallidum* Jackson, 1913.

General discussion

The quality of SRS data: how accurate are they?

The species used to illustrate habitat profiles were selected at random. Until more data are analysed it is difficult to determine which species will provide the most useful and informative examples. Some profiles are difficult to interpret and it may be thought that the quality of the data is suspect. There are at least four possible sources of error to consider: (1) it is known that from time to time species may be misidentified; (2) the recorded field data may be too poor or insufficient to know precisely to which habitat category it should be assigned; (3) some errors may have been made by converting the SRS 36-habitat category classifications to 21; (4) did recorders always collect at random or was there significant bias by searching for certain species or by collecting in only a few preferred habitats?

Comments on the above are as follows:

1. Incorrect identifications have been made from time to time and if a common species is mistaken for a rarity for which few records are available, the profile could be falsified. Nevertheless, it is equally possible that rare species are sometimes misidentified as common species. It is unlikely that any of the species mentioned in this text have been subject to a serious error of this type.
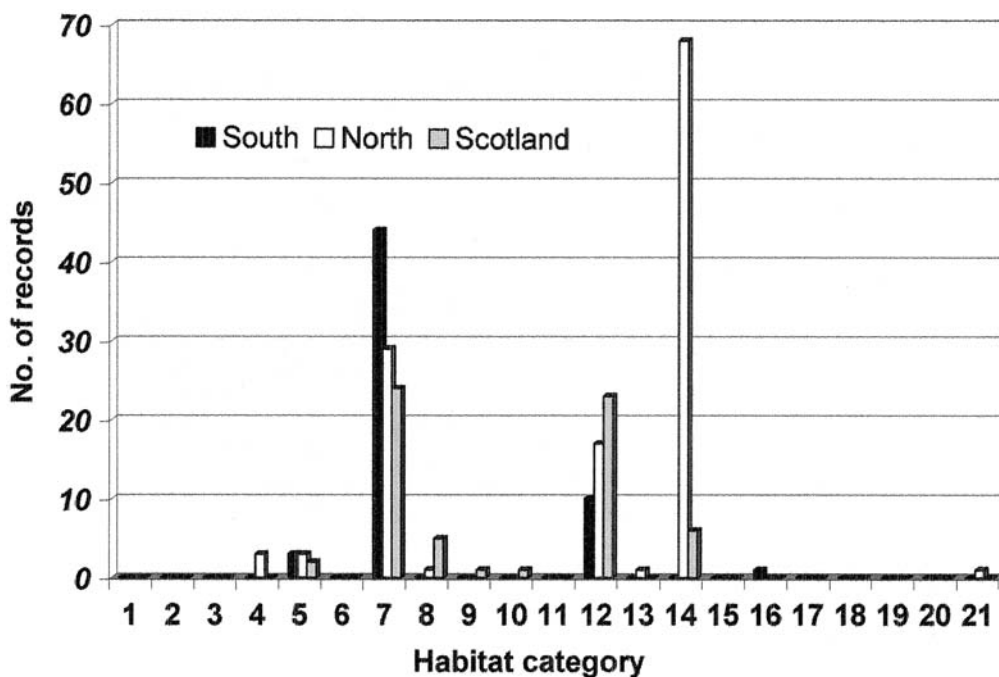
Fig. 16: Habitat profile of *Hypselistes jacksoni* (O. P.-Cambridge, 1902).
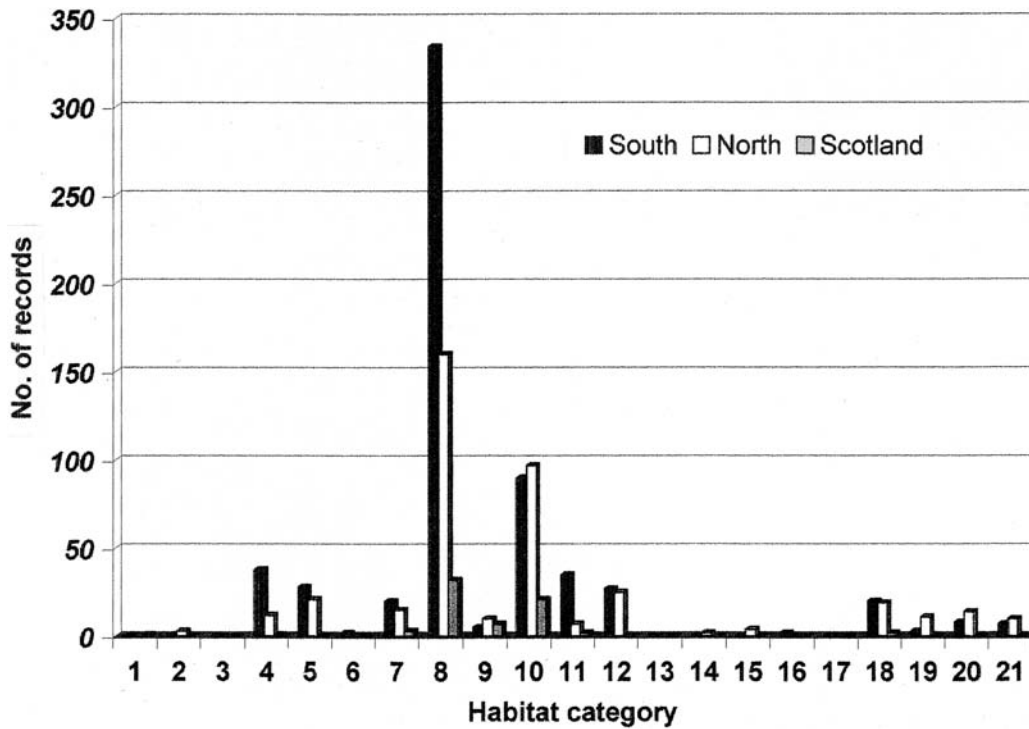
Fig. 17: Habitat profile of *Linyphia hortensis* Sundevall, 1830.

Most of these species have a large number of records in the database and the risk of misidentification is probably small.

2. Poor field recording of habitats is always possible, perhaps more so with some of the older records. However, most records in the SRS used in this analysis are relatively recent and most present-day recorders are more accurate.

3. Some errors may have occurred by reducing the 36 habitat categories of the SRS to 21, and resolving this problem is difficult. The SRS category "Rock, scree and cliff" may have included both inland rocky areas and coastal rocks and cliffs. These have been separated in the 21-habitat category system and the SRS data assumed to refer mainly to inland areas. A few SRS categories are ambiguous and sometimes the records were difficult to assign accurately to the 21-category classification.

4. Bias in collecting is thought to be negligible because it occupies so little of the recorder's time. However, some habitats may be preferred for collecting as they are known to be richer or are closer to home.

The evidence suggests that the profiles are as accurate as can be achieved by the precautions taken. No system
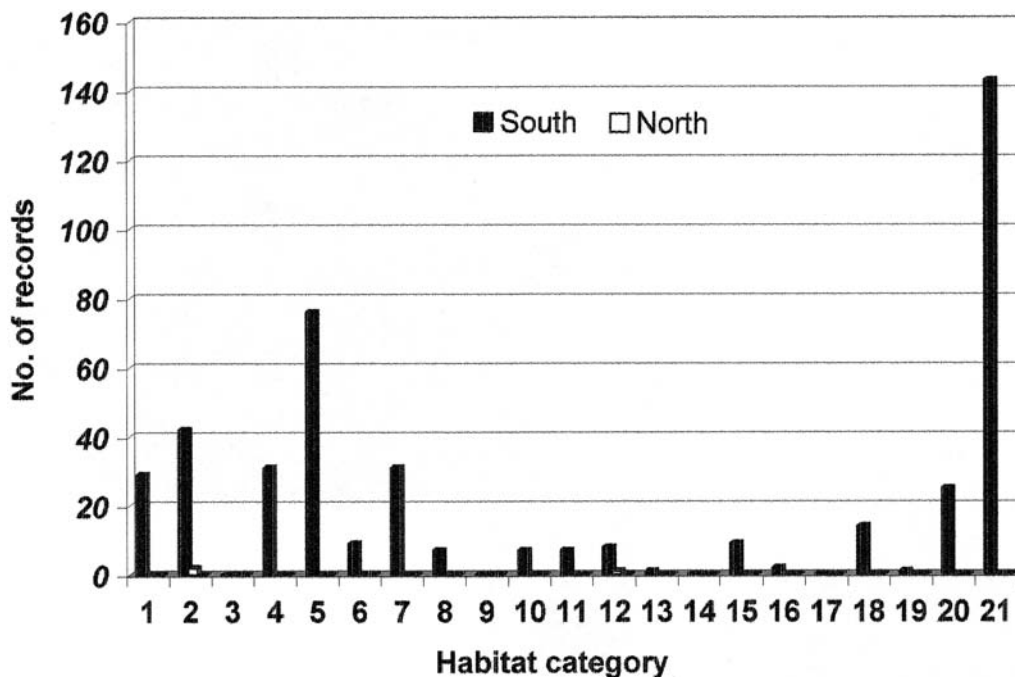
Fig. 18: Habitat profile of *Xysticus kochi* Thorell, 1872.
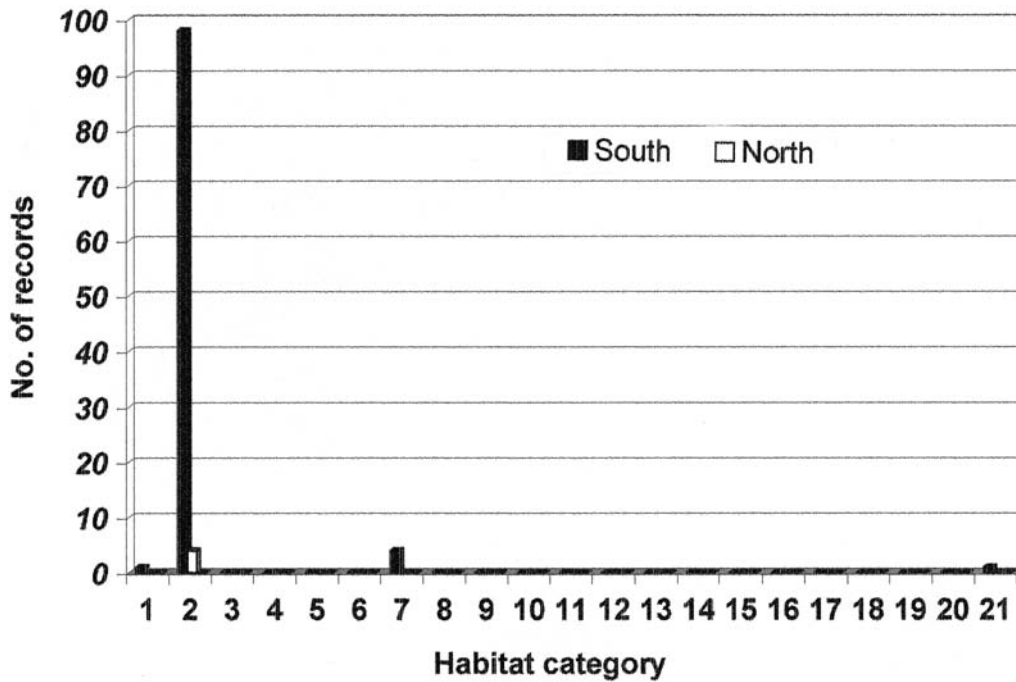
Fig. 19: Habitat profile of *Sitticus saltator* (O. P.-Cambridge, 1868).

is faultless but the SRS data are probably as good as the procedure adopted permits and should improve in the future. Nevertheless these possible errors emphasise the need for accurate habitat recording and confirmation of identification when dealing with difficult species.

Habitat profiling using data in the British Arachnological Society's Spider Recording Scheme was only possible because the scheme had developed a computerised data bank based on MAPMATE, the existence of the six-figure National Grid References and also vice-counties (P. R. Harvey, pers. comm.). This made it possible to extract very quickly habitat records from the three regional areas (South England, North England and Scotland) and assign them to a prepared habitat classification representing the British environment. Britain may be too small an area for an exercise to assess regional habitat differences, but it has the advantage of fewer habitat variables compared with larger countries further south in Europe. This helps to make the profiles more precise and less complicated.

Although the collection of data was random and probably unbiased there may be other problems. Mis-identification undoubtedly takes place but it can be avoided by profiling only those species for which this problem is thought to be unlikely. An unknown possible error is the reliability of habitat descriptions for some of
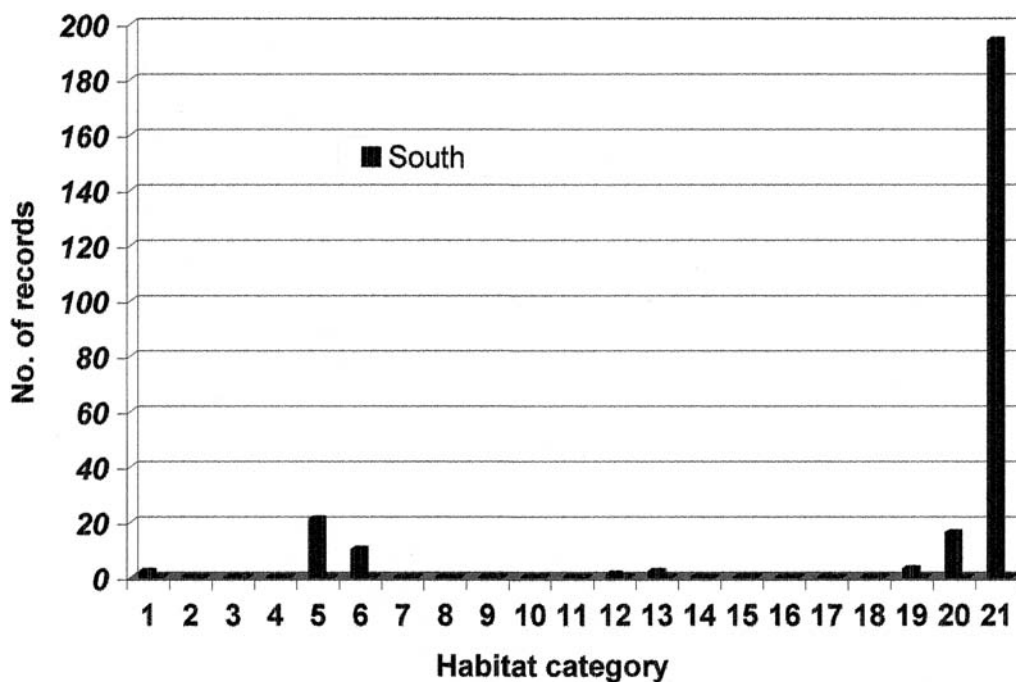
Fig. 20: Habitat profile of *Zodarion italicum* (Canestrini, 1868).
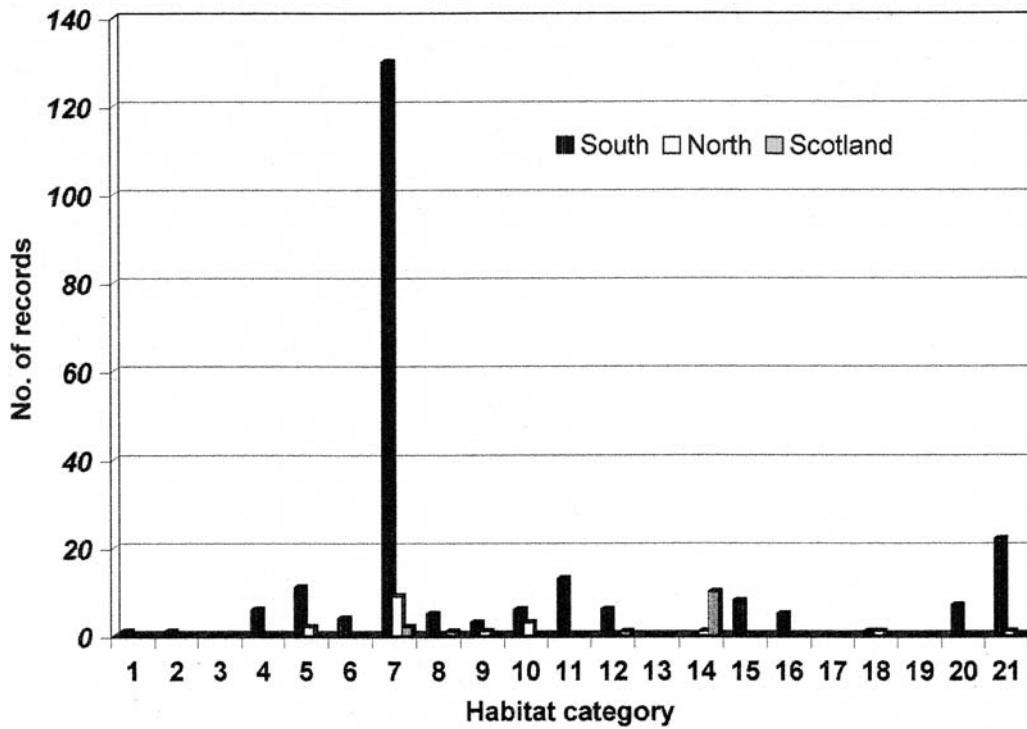
Fig. 21: Habitat profile of *Simitidion simile* (C. L. Koch, 1836).

the older records. If the field data were not clear or ambiguous, the record may have been placed in an incorrect habitat category. There is no means of assessing this but it may be possible to minimise the risk by using only recent records, perhaps limiting them to the last 20 years, if numbers are sufficient.

Conclusions

In spite of possible imperfections in the data the SRS habitat records are the only material available to test the methodology of habitat profiling. Even if the profiles are only approximately accurate this should be sufficient to detect trends. The paper discusses the following main points:

1. The importance of constructing an ecologically realistic habitat classification for which each category is carefully defined.

2. The selection of those species numerous enough to avoid bias and minimise other possible imperfections in the data.

3. The profiling of species which occur in different geographical regions to discover whether habitat preferences differ from one region to another.
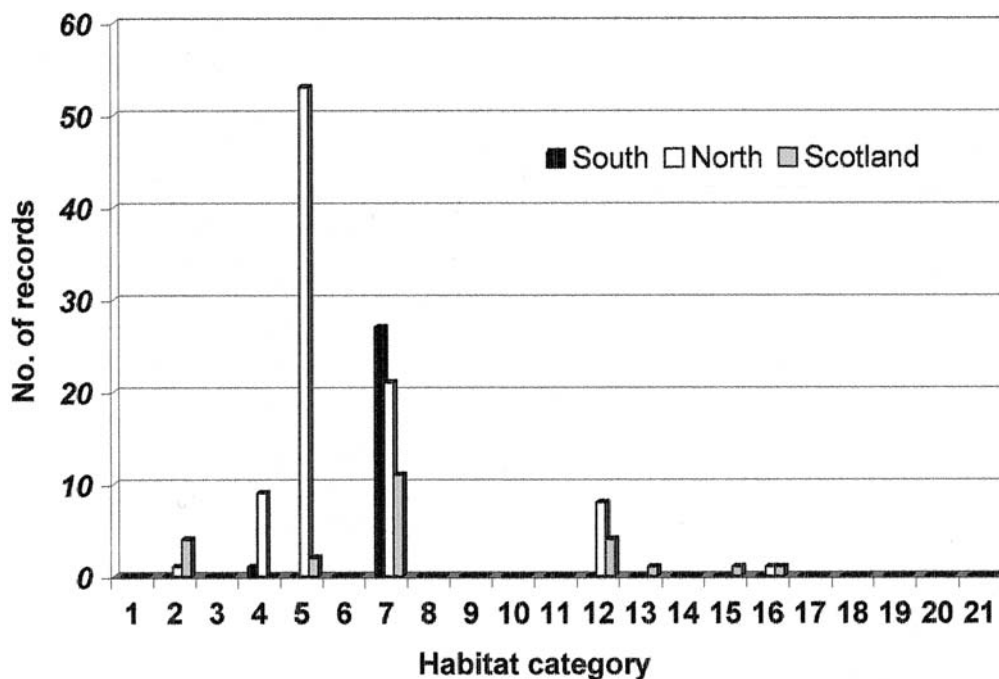
Fig. 22: Habitat profile of *Leptopthrix hardyi* (Blackwall, 1850).
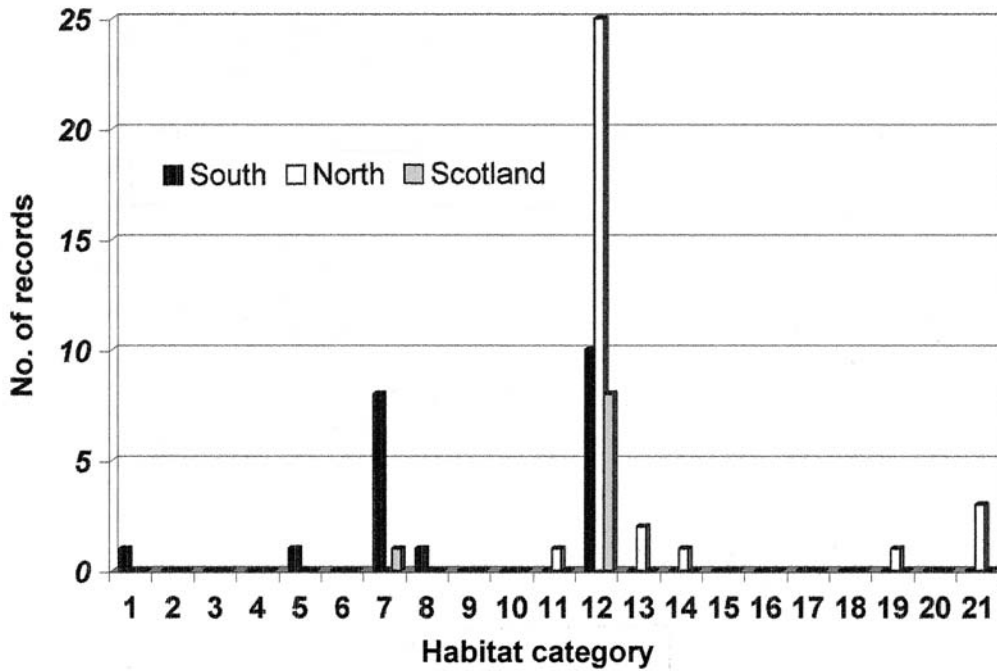
Fig. 23: Habitat profile of *Argyroneta aquatica* (Clerck, 1757).

4. It is suggested that arachnologists in other European countries should adopt a similar method using their own habitat classification systems because habitat profiling has the potential to become an unbiased, quantitative method to illustrate habitat preferences and how they differ across Europe.

The few habitat profiles described in this paper include some species which show hardly any difference in habitat preference from south to north, and others which may have small but clear differences. The former are mainly confined to the few stenotopic species while the meso/eurytopic species, being more habitat-tolerant,

appear to exploit whichever habitats are most typical or widespread in the region in which they occur. In this respect collectors may introduce a bias by spending more time in these habitats because they are more common and easier to find.

In this paper the chosen method to demonstrate habitat profiles is by arranging the data in the form of histograms. This method is preferred because the actual totals of records are included and the height of the columns clearly indicates the most favoured habitats. Nevertheless it has been suggested to me that pie-charts might be a better method of demonstrating habitat
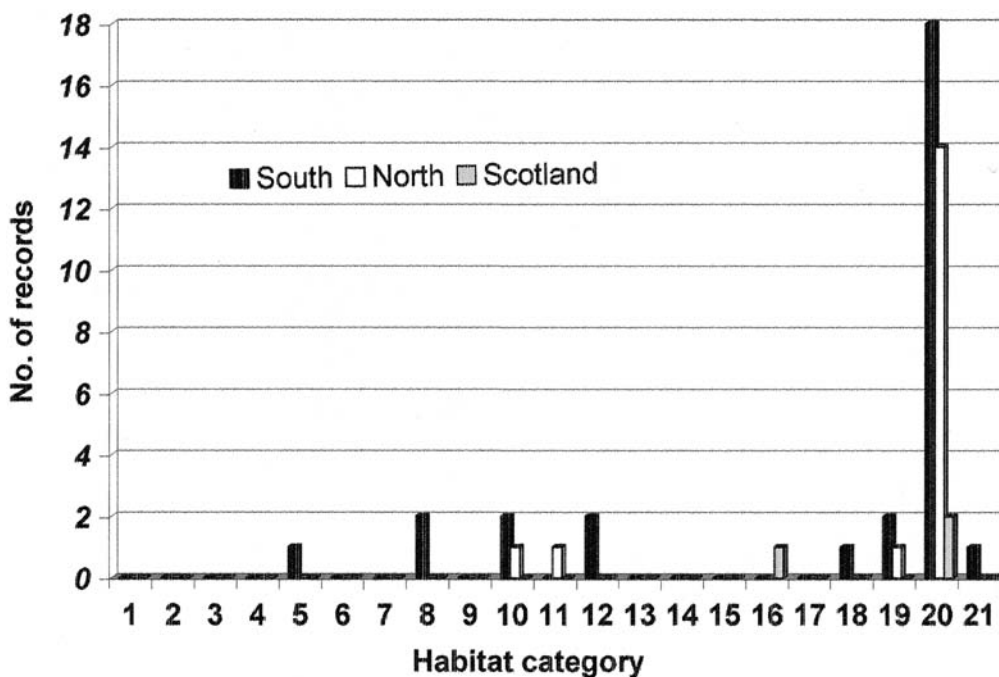
Fig. 24: Habitat profile of *Achaearanea tepidariorum* (C. L. Koch, 1841).
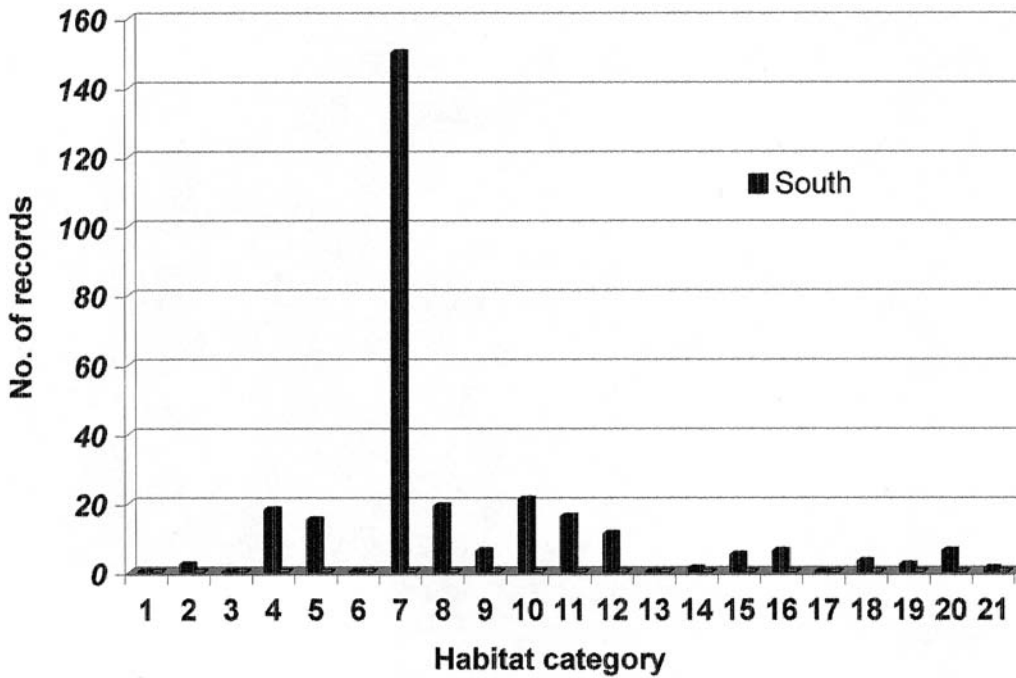
Fig. 25: Habitat profile of *Mangora acalypha* (Walckenaer, 1802).

profiles. Personally I feel that the subject needs much more discussion and further analysis of the data before there can be a consensus on the best method of profiling.

It is reasonable to assume that during the course of evolution a species becomes adapted to those environments where it is most successful: ample food supply, fewer competitors and breeding success maintaining the population. This adaptation is likely to persist in those environments which change very little over long periods of time, such as coastal dunes and saltmarshes, mountain tops, bogs or marshes originating from glacial relics such as kettle holes and pingoes, and some long-established open habitats similar to the sandy Breckland

heaths of Norfolk and Suffolk. Some of the stenotopic profiles are examples of these species. However, most natural and semi-natural habitats are constantly changing either in relation to plant succession, changing weather patterns or disturbance by man or wild animals. For most species it is clearly an advantage to be more habitat-tolerant so that as one habitat becomes less favourable they can easily adapt to an alternative. Those species which are said to be spreading to new areas due to global warming are demonstrating an ability to exploit new environments. Wicken Fen National Nature Reserve in Cambridgeshire is a good example of the influence of habitat change (Friday, 1997; Duffey, 2008).
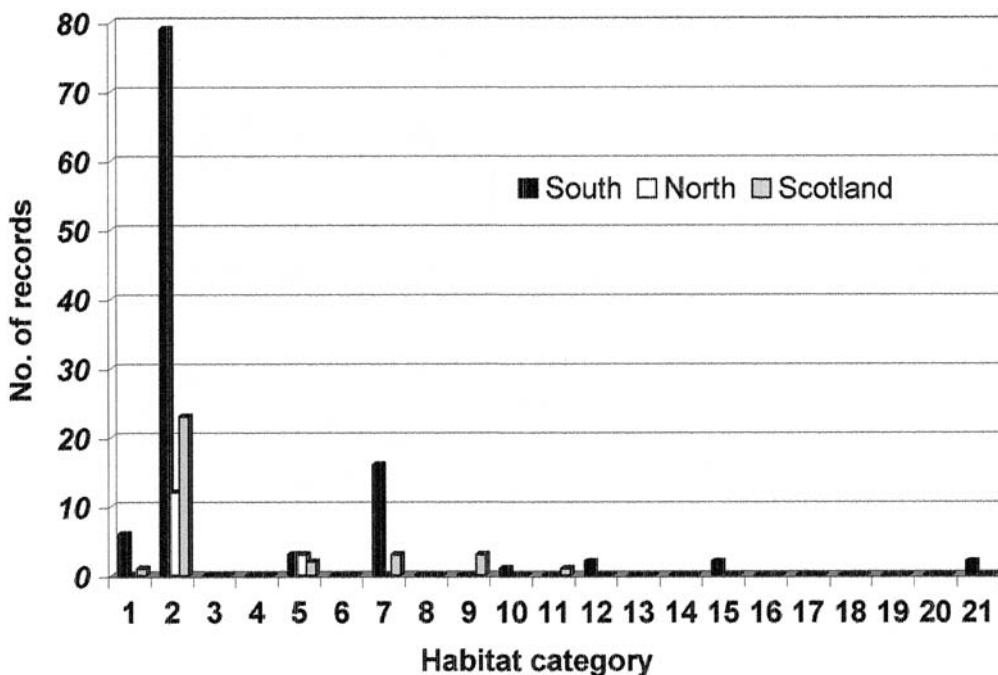
Fig. 26: Habitat profile of *Zelotes electus* (C. L. Koch, 1839).
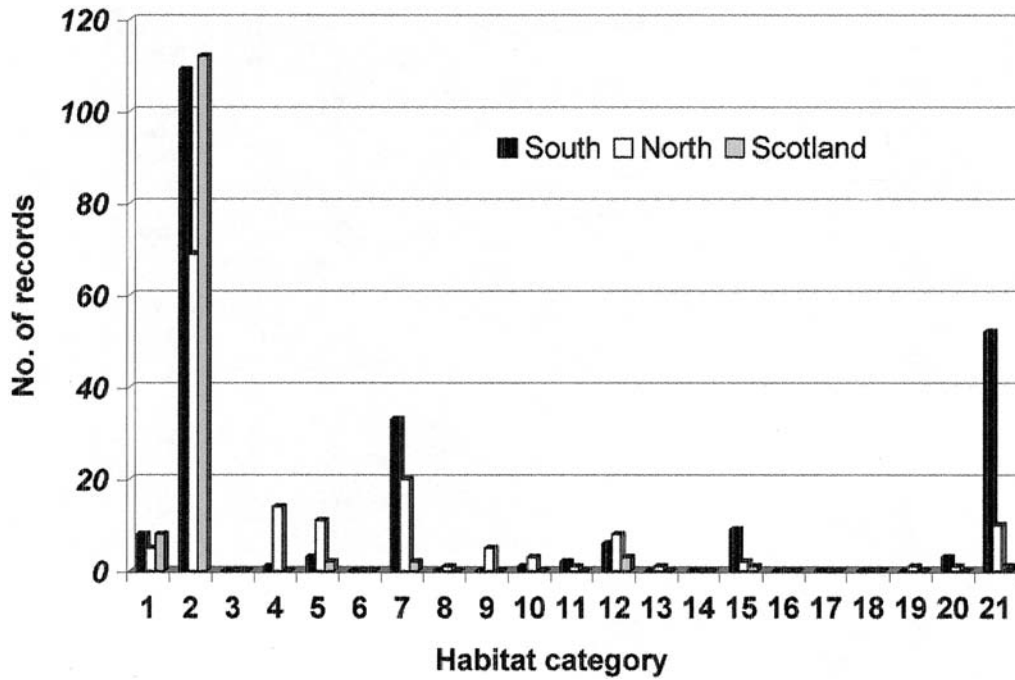
Fig. 27: Habitat profile of *Arctosa perita* (Latreille, 1799).

This fen has been a nature reserve for over 100 years, during which time it has been through many changes including long periods of dryness. As vegetation and soil moisture were modified several rare species were lost though others survived. It seems most likely that man's modification of the British landscape over the last two to three thousand years has allowed the most adaptable spider species to survive as they are now the most common, while the habitat-intolerant specialists have declined as their limited environments have been reduced and become more isolated. This process continues.
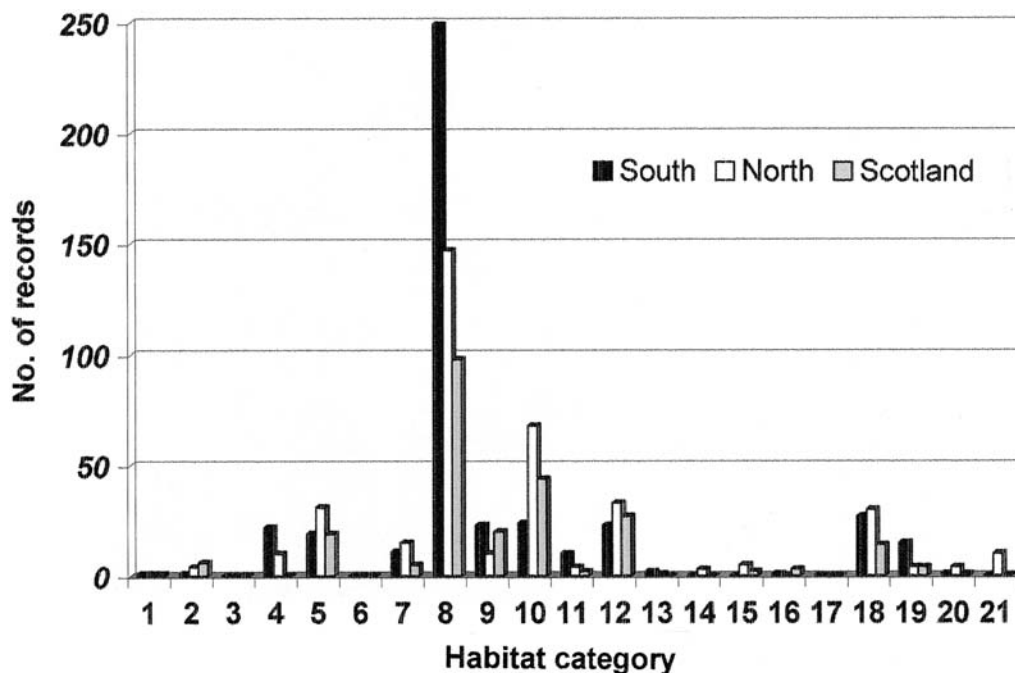
Fig. 28: Habitat profile of *Diplocephalus latifrons* (O. P.-Cambridge, 1863).

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Appendix 1

Total numbers of records derived from the BAS Spider Recording Scheme for each habitat category for each of the 28 species used as examples. Habitat categories as in Table 1. SE=South England, NE=North England, Sco=Scotland.

| Species		1	2	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Tenuiphantes tenuis	SE	106	170	630	420	9	162	585	58	132	138	261	31	0	33	7	2	646	168	110	269
	NE	32	72	208	295	8	137	212	36	165	25	175	6	42	39	3	3	94	11	71	91
	Sco	39	144	6	193	3	65	105	39	109	18	88	1	3	30	8	2	87	16	8	10
Tenuiphantes zimmermanni	SE	6	9	105	58	3	132	927	75	228	69	139	0	0	19	5	2	47	14	4	13
	NE	6	12	85	90	9	161	444	101	176	24	125	17	175	52	19	3	48	5	11	28
	Sco	15	23	2	66	4	238	411	554	197	16	116	3	23	19	89	2	24	3	2	8
Erigone atra	SE	32	42	200	254	3	172	239	23	63	53	212	10	0	5	5	0	486	5	31	185
	NE	28	24	108	255	15	117	90	25	92	21	131	7	17	20	18	0	72	14	31	47
	Sco	25	125	1	136	0	35	33	12	34	8	77	0	3	4	10	0	32	4	1	1
Erigone dentipalpis	SE	13	22	118	141	9	98	123	13	39	47	111	5	0	6	3	0	407	143	29	158
	NE	18	24	89	230	7	60	58	8	37	12	71	4	9	15	11	0	36	7	8	23
	Sco	16	78	3	118	0	21	40	11	26	5	39	1	1	1	15	0	36	3	1	1
Saaristoa abnormis	SE	1	0	26	22	0	64	97	14	21	12	36	0	0	2	0	2	8	0	0	1
	NE	0	0	60	23	3	58	49	7	25	4	34	3	58	3	8	0	1	0	0	1
	Sco	3	4	0	16	1	130	142	156	42	2	71	1	0	10	17	1	0	0	0	1
Ceratinella brevipes	SE	1	5	26	13	1	76	34	4	2	6	22	0	0	3	1	0	4	0	0	0
	NE	0	9	43	40	4	129	28	14	22	5	77	6	83	0	11	0	0	0	0	1
	Sco	1	42	1	35	2	146	74	87	50	6	90	0	8	2	16	0	0	0	0	3
Gonatium rubens	SE	3	2	124	50	1	117	32	7	21	45	41	1	0	6	7	0	15	3	1	6
	NE	2	21	88	65	9	189	73	30	54	14	83	6	121	16	17	0	4	2	0	5
	Sco	7	27	3	76	2	257	69	49	53	14	115	2	15	7	30	0	2	0	0	5
Enoplognatha ovata	SE	7	15	191	150	4	94	445	28	136	165	136	3	0	8	1	0	150	53	44	91
	NE	10	21	42	112	14	71	161	40	125	58	81	12	14	26	0	1	69	22	24	61
	Sco	11	22	2	40	1	24	56	22	61	19	33	4	4	3	0	0	31	4	3	4
Bathyphantes gracilis	SE	38	46	298	215	3	134	318	29	71	74	297	34	0	13	3	0	361	89	11	40
	NE	14	27	82	186	12	117	86	14	52	16	171	17	149	9	19	0	35	9	14	27
	Sco	16	105	1	108	3	66	82	24	41	10	168	8	28	3	5	2	32	3	0	6
Alopecosa pulverulenta	SE	18	41	260	238	26	123	137	9	33	50	57	1	0	15	4	0	208	29	20	164
	NE	4	33	175	146	20	119	40	22	23	11	78	0	31	35	9	0	5	8	11	31
	Sco	20	59	1	137	1	193	56	92	19	13	101	0	2	6	102	0	2	0	0	0
Centromerita bicolor	SE	6	7	50	74	1	21	14	2	4	8	24	1	0	2	0	0	139	34	4	14
	NE	9	11	38	101	3	85	24	2	10	1	53	1	40	3	15	0	22	0	3	19
	Sco	7	79	2	95	0	32	38	13	9	5	75	8	1	5	36	0	17	3	1	5
Maso sundevalli	SE	0	11	39	26	0	46	286	11	77	43	53	1	0	5	1	0	24	11	2	8
	NE	0	4	13	8	1	40	108	15	40	5	42	6	8	8	0	0	3	1	1	2
	Sco	2	5	0	4	0	21	51	14	38	4	34	0	5	1	0	0	2	0	0	0
Talavera aequipes	SE	2	2	29	22	3	36	1	0	0	1	4	0	0	6	4	0	4	0	9	68
	NE	0	1	19	3	0	6	0	0	1	0	1	0	0	1	0	0	0	1	0	1
	Sco	1	5	0	1	0	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0
Centromerus arcanus	SE	0	0	0	1	0	11	1	0	1	0	1	0	0	0	0	0	0	0	0	0
	NE	0	0	9	4	0	10	7	22	8	0	25	4	51	0	1	0	0	0	0	0
	Sco	0	0	0	1	0	32	19	102	41	0	32	0	6	0	3	0	0	0	0	1

Species		Habitat categories																			
		1	2	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Porrhomma pallidum	SE	0	0	0	1	0	4	7	4	5	0	0	0	0	0	1	0	0	0	0	0
	NE	0	1	0	1	0	10	21	22	16	0	4	0	0	1	2	0	1	0	0	1
	Sco	0	5	0	5	0	21	29	93	13	0	24	0	2	2	7	0	0	0	0	1
Hypselistes jacksoni	SE	0	0	0	3	0	44	0	0	0	0	10	0	0	0	1	0	0	0	0	0
	NE	0	0	3	3	0	29	1	0	0	0	17	1	68	0	0	0	0	0	0	1
	Sco	0	0	0	2	0	24	5	1	1	0	23	0	6	0	0	0	0	0	0	0
Linyphia hortensis	SE	0	1	38	28	2	20	334	5	90	35	27	0	0	0	2	0	20	3	8	7
	NE	0	3	12	21	0	15	160	10	97	7	25	0	2	4	0	0	19	11	14	10
	Sco	1	0	1	0	0	3	32	7	21	2	0	0	0	0	0	0	2	0	0	0
Xysticus kochi	SE	29	42	31	76	9	31	7	0	7	7	8	1	0	9	2	0	14	1	25	143
	NE	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Sco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sitticus saltator	SE	1	98	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	NE	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zodarion italicum	SE	2	0	0	21	10	0	0	0	0	0	1	2	0	0	0	0	0	3	16	194
	NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simitidion simile	SE	1	1	6	11	4	130	5	3	6	13	6	0	0	8	5	0	1	0	7	22
	NE	0	0	0	2	0	9	0	1	3	0	0	0	1	0	0	0	1	0	0	1
	Sco	0	0	0	0	0	2	1	0	0	0	1	0	10	0	0	0	0	0	0	0
Leptothrix hardyi	SE	0	0	1	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NE	0	1	9	53	0	21	0	0	0	0	8	0	0	0	1	0	0	0	0	0
	Sco	0	4	0	2	0	11	0	0	0	0	4	1	0	1	1	0	0	0	0	0
Argyroneta aquatica	SE	1	0	0	1	0	8	1	0	0	0	10	0	0	0	0	0	0	0	0	0
	NE	0	0	0	0	0	0	0	0	0	1	25	2	1	0	0	0	0	1	0	3
	Sco	0	0	0	0	0	1	0	0	0	0	8	0	0	0	0	0	0	0	0	0
Achaearanea tepidariorum	SE	0	0	0	1	0	0	2	0	2	0	2	0	0	0	0	0	1	2	18	1
	NE	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	14	0
	Sco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
Mangora acalypha	SE	0	2	18	15	0	150	19	6	21	16	11	0	1	5	6	0	3	2	6	2
	NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zelotes electus	SE	6	79	0	3	0	16	0	0	1	0	2	0	0	2	0	0	0	0	0	2
	NE	0	12	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sco	1	23	0	2	0	3	0	3	0	1	0	0	0	0	0	0	0	0	0	0
Arctosa perita	SE	8	109	1	3	0	33	0	0	1	1	6	0	0	9	0	0	0	0	3	52
	NE	5	69	14	11	0	20	1	5	3	1	8	1	0	2	0	0	1	0	1	12
	Sco	8	112	0	2	0	2	0	0	0	0	3	0	0	1	0	0	0	0	0	1
Diplocephalus latifrons	SE	1	1	22	19	0	11	249	23	24	10	23	2	0	0	1	0	27	15	1	0
	NE	1	4	10	31	0	15	147	10	66	4	33	1	3	5	0	0	30	4	4	11
	Sco	1	6	0	19	0	5	98	20	44	2	27	0	0	2	3	0	14	4	1	1