Spider (Arachnida: Araneae) communities of riparian gravel banks in the northern parts of the European Alps

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Summary

A comprehensive investigation of the gravel bank spider fauna of 10 rivers and streams in the northern parts of the European Alps provided an account of 45 species in 13 families. The most common species were *Pardosa wagleri, Erigone atra* and *Oedothorax agrestis*. In combination with six previously published studies on spiders of flood plain habitats, a set of 60 species, that are "common or dominant" on riparian gravel banks, was identified and grouped in four categories: riparian, open land, forest, and euryoecious. *Pardosa wagleri, Pardosa saturatior, Pirata knorri*, and *Oedothorax agrestis* were classified as stenoecious riparian species. Altitude, floodplain width and level of human impact had no influence on the number of species recorded in each river section. The stenoecious riparian species do not appear to be suitable indicators for a natural river system, since there is no evidence that their numbers are affected by the artificial reduction in number and size of floodplain gravel banks.

Introduction

In Central Europe, alpine rivers are characterised by a highly variable discharge rate, with peak floods occurring mainly in spring. The sediment load in the upper catchment of these rivers consists mainly of large rocks and gravel. Constrictions in the river floodplain cause this gravel to accumulate, thereby forming large braided gravel beds. During a peak flood, this gravel is moved and vegetation destroyed (e.g. Aulitzky, 1980; Karl & Mangelsdorf, 1975; Mangelsdorf & Scheuermann, 1980). Floods therefore pose a threat to the survival of many typical organisms that inhabit this environment. However, these organisms are also dependent on floods to maintain specific habitat qualities, such as a substrate made up of loose sand and gravel, and no or only a sparse vegetation cover.

A specifically adapted arthropod community inhabits this highly dynamic environment. Among the most dominant members of the riparian gravel bank fauna are spiders, and in particular wolf spiders (Lycosidae) (Manderbach & Reich, 1995; Smit *et al.*, 1997; Steinberger, 1996, 1998; Manderbach, 1998). They are thought to have evolved a number of characteristics in response to this dynamic river environment, such as the use of polarised light for orientation (Papi, 1959; Papi & Tongiorgi, 1963) and seasonal movements (Framenau *et al.*, 1996a). The mobile brood care of wolf spiders appears to be favoured in an environment which is characterised by frequent inundation (Framenau, 1995; Churchill, 1998).

Today man-made weirs, dams, and embankments control most floodplains in Central Europe (Baxter, 1977; Petts *et al.*, 1989). These constructions have changed the natural river system dynamics and affect, in particular, the occurrence of vegetation-sparse or -free gravel banks, which are now mainly restricted to the upper catchment of large alpine rivers. Only remnant gravel banks can be found in the lower floodplains (Fabrice & Michel, 1992; Plachter, 1993). The number and size of gravel banks in small streams seems to be similarly reduced (Hering *et al.*, 1997).

While a number of studies have investigated the spider communities of floodplains, they have not included riparian gravel banks (e.g. Uetz, 1976; Moring & Stewart, 1994; Bell *et al.*, 1999). Only one study comprehensively characterises a whole floodplain spider community (Steinberger, 1996). This study provides a detailed account of the habitat requirements of most spider species encountered at the Lech River in Austria, but was limited to one river. Most studies that have specifically examined gravel banks, have mainly been limited to single rivers (e.g. Plachter, 1986; Dröschmeister, 1994; Hering, 1995; Smit, 1997; Heidt *et al.*, 1998; Steinberger, 1998; Zulka *et al.*, 1998). Only two autecological studies have dealt with spider species that are characteristic of riparian gravel banks (Albert & Albert, 1976; Framenau *et al.*, 1996a,b).

Our study provides a comprehensive account of the spider fauna of Central European gravel bank flood plains. Samples taken at ten different rivers have been incorporated with previously published studies to determine a set of the most "common or dominant" riparian spider species. These are classified according to habitat requirements. Collections from river sections with and without human impact aimed to demonstrate the effects of hydrological engineering on the composition of the spider communities, and the suitability of riparian spiders as indicators of a natural river system is discussed.

Methods

The ecological characterisation of the riparian gravel bank spider fauna is based on a survey of 10 alpine rivers and streams and a review of six major previous studies including one conducted outside the alpine region.

Fourteen floodplain sections belonging to 10 rivers and streams in three main river systems in the northern parts of the European Alps were investigated during three surveys in May/June, July/August and October 1995 (Fig. 1, Table 1). These sections represented a wide variety from large rivers to small streams which differed not only in the amount and size of gravel bars but also in the level of human impact on discharge and sediment load. The sample programme included the largest natural braided river section in the northern parts of the

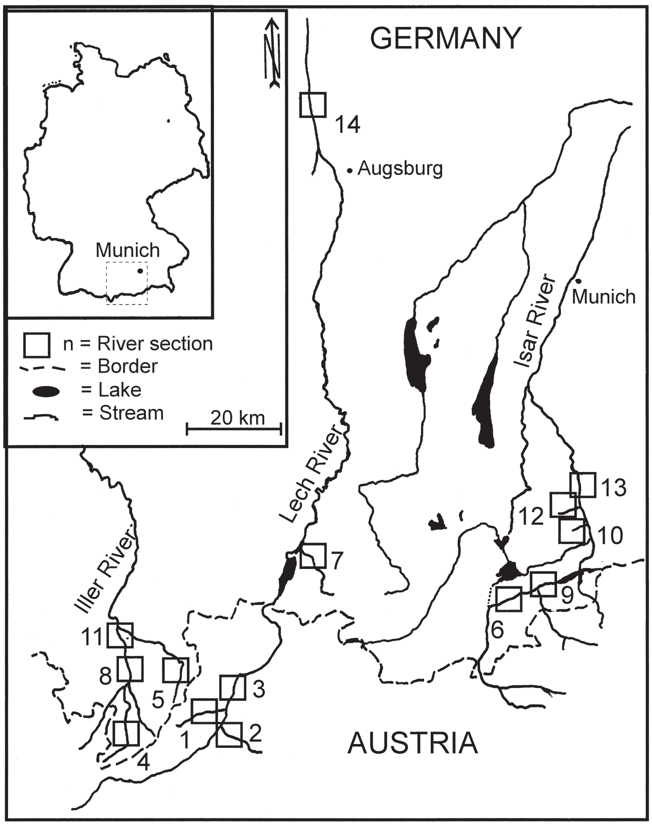

Fig. 1: Sampling sites. Hornbach (1), Streimbach (2), Lech near Forchach (3), Stillach (4), Ostrach (5), Isar near Schröfeln (6), Halblech (7), Iller near Rubi (8), Isar near Vorderriss (9), Schwarzenbach (10), Iller near Sonthofen (11), Arzbach (12), Isar near Arzbach (13), Lech near Langweid (14).

European Alps (Lech River near Forchach: Fig. 1 [3]), large rivers considerably affected by weirs and embankments (e.g. Lech River near Langweid [14]) and small streams in a more or less natural condition (e.g. Schwarzenbach [10]). Each river was assigned to one of three categories depending on the level of human impact: natural condition, minor and major human impact (Table 1).

The composition of the spider communities was investigated by standardised time samples (Herold, 1928, 1929; Andersen, 1969; Plachter, 1986). On vegetation-free gravel banks in a strip about 0.5–1 m wide along the water edge, the fine substrate was combed with fingers and larger stones were turned over. All arthropods, except Apterygota, were caught: smaller ones with an aspirator, larger ones with forceps. The specimens were transferred into 70% ethyl alcohol. Each floodplain section was sampled for a total of 120 min per survey. This sampling time was divided into 6 periods of 20 min on consecutive gravel banks. The lengths of the sampled areas varied between 5 and 25 m depending on the substrate and the number of animals encountered (details in Manderbach, 1998).

Six previous studies on flood plain spider communities in which data were obtained by "hand-collecting" (time or area limited) were included in the analysis (Table 4). Within these studies, data not obtained on vegetation-free gravel banks or by a different method (e.g. pitfall trapping) were not taken into account in our study.

Species which were found in more than 10% of all river sections or which represented more than 5% of the total catch in one section were called "common or dominant" species. Only these species were considered in describing the typical gravel bank spider communities of alpine rivers. These species were grouped in one of four categories: riparian, open land, forest and euryoecious. The categories "riparian" and "open land" comprise three sub-categories each. The categorisation followed standard publications on the ecology of Central European spider species (Maurer & Hänggi, 1990; Heimer & Nentwig, 1991; Hänggi *et al.*, 1995).

Results

A total of 1,698 spiders were collected in 14 river sections, including 474 (28%) adult spiders belonging to 45 species in 13 families (Table 2). Overall, they comprised 15% of all arthropods encountered (Fig. 2). Five families (Amaurobiidae, Anyphaenidae, Philodromidae, Salticidae and Tetragnathidae) were represented only by juvenile spiders. Most species (22) belonged to the family Linyphiidae. More than half of all species (26; 58%) were found in only one river section. The wolf spider *Pardosa wagleri* was the most common species, found in 11 of 14 sections. *Erigone atra* and *Oedothorax agrestis* were represented in 9 river sections. The spider communities were dominated by only a few species. Five species (*Erigone atra, E. dentipalpis, Oedothorax agrestis, Pardosa wagleri* and *Pirata knorri*) represented more than 75% of the total catch of all adult spiders.

We found no evidence that altitude (ANOVA, $F_{11,2}=0.93$, $p>0.5$), floodplain width (ANOVA, $F_{3,10}=0.5$, $p>0.5$), or the level of human impact (ANOVA, $F_{2,11}=0.898$, $p>0.1$) had an influence on the number of species found in any of the river sections.

The largest number of adult spiders per sample was found at the Schwarzenbach, the lowest at the Iller near Sonthofen (Table 3). Floodplain width and level of human impact showed no influence on the total numbers of adult spiders encountered, nor on the numbers of any of the typical gravel bank species *P. wagleri, P. saturatior, P. knorri* and *O. agrestis*. Altitude appeared to affect only the numbers of adult *P. saturatior* (ANOVA, $F_{1,12}=4.904$, $p<0.05$), a species that is restricted to higher elevations.

In combination with the previously published studies, 60 "common or dominant" species were identified and were considered in the characterisation of the European spider communities of riparian gravel banks (Table 4).

Discussion

Spider communities of riparian gravel banks

Riparian species

The spider community on the shore line of rivers does not appear to be very specific. Only 10 (17%) of the "common or dominant" species have their main distribution on the banks of rivers and streams and seem to be almost exclusively "riparian". However, seven of these ten species can occasionally be found in habitats that share similar qualities with riparian gravel banks, such as rocky outcrops and gravel pits. These may not be located in river floodplains and therefore lack the proximity of running water. Therefore, the riparian species can be divided into three groups depending on the degree of their affinity to running water: stenoecious riparian species (with a strong affinity to running water), species of gravel bars (with limited affinity to running water) and species of lake shores.

Only *Pardosa saturatior, Pardosa wagleri, Pirata knorri* and *Oedothorax agrestis* can be classified as stenoecious riparian species. They seem to be restricted to the shores of running waters, where they can reach very high densities. *Pardosa wagleri* is the commonest species on riparian gravel banks and was found in eleven of the 14 investigated river sections. Above an altitude of approximately 900 m it is accompanied by its slightly larger sibling species *Pardosa saturatior* (Barthel & Helversen, 1990). Both species coexist on gravel banks between 980 m and 1000 m. *Oedothorax agrestis* has not only been recorded on gravel banks. Single individuals have been found in other floodplain habitats, e.g. alder woodland (Nentwig, 1983) and on muddy soil (Palmgren, 1976). Steinberger (1996) found this species mainly near the edge of a river, but a few individuals were also collected in muddy areas at some distance from the water. However, its affinity to water appears to be strong.

Five species (*Janetschekia monodon, Clubiona similis, Arctosa cinerea, Caviphantes saxetorum* and *Diplocentria mediocris*) can regularly be found on riparian gravel banks but they display only a limited affinity to running water. They have also repeatedly been recorded in areas without adjacent streams or rivers. It appears that the species of this group prefer rocky areas without vegetation cover. These habitat qualities are maintained by the dynamic water regime in gravel bed floodplains but can also be found in other circumstances. *Janetschekia monodon* has been collected in gravel habitats near the edge of glaciers (Thaler, 1969). *Clubiona similis* is generally known from "moist areas with low vegetation" (Heimer & Nentwig, 1991). Steinberger (1996) encountered *C. similis* on xerothermic gravel banks with sparse vegetation. *Caviphantes saxetorum* seems to migrate seasonally between areas with large stones near the water in September and dry areas covered by small stones in June (Cooke & Merrett, 1967). However, this

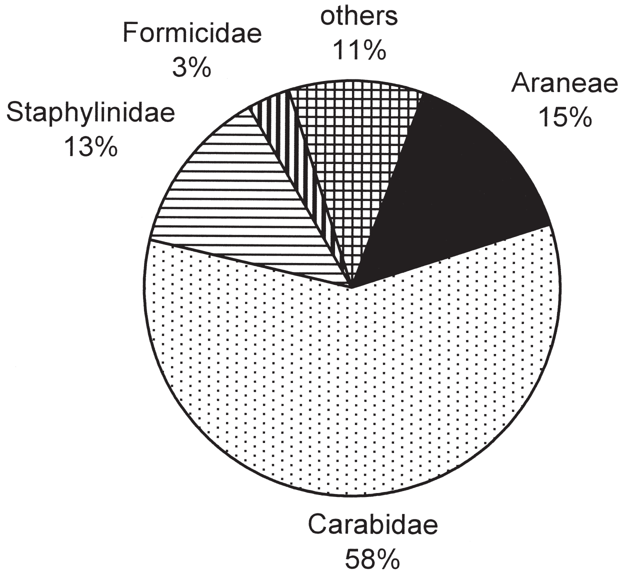

Fig. 2: Composition of the riparian arthropod communities in gravel bed floodplains of the European Alps (n=11,645).

No. in Fig. 1	River (location)	Altitude (m) a.s.l.	Description	Floodplain width	Human impact
1	Hornbach	1000	Large braided section above gorge (dam)	>100 m	1
2	Streimbach	980	Mainly only one channel; high water velocity	10–50 m	0
3	Lech (near Forchach)	910	Largest braided river section in northern European Alps; large gravel banks; large areas with sparse vegetation between gravel banks and forest	>100 m	0 (e)
4	Stillach	900	Large braided section above gorge	>100 m	0 (e)
5	Ostrach	860	Single stream bed; high inclination	10–50 m	0
6	Isar (near Schröfeln)	810	Large braided floodplain section; large gravel banks; vegetation cover increasing over recent years; below Krün Weir	10–50 m	1 (w)
7	Halblech	770	Undivided stream; small gravel banks; coarse substrate and sludge; algal growth	10–50 m	2 (ee)
8	Iller (near Rubi)	770	Largest gravel banks along Iller River; bedrock on east bank; adjacent forest	51–100 m	2 (e)
9	Isar (near Vorderriss)	770	Largest, most natural braided floodplain section in German Alps; large gravel banks; below Krün Weir	>100 m	0 (w)
10	Schwarzenbach	760	Small tributary to Isar River below Sylvenstein Reservoir; small gravel banks; completely shaded by riparian forest	<10 m	0
11	Iller (near Sonthofen)	720	Small, isolated gravel banks; coarse substrate and sludge, relicts of riparian forest	10–50 m	2 (ee)
12	Arzbach	700	Small tributary to Isar River; small gravel banks; partly shaded by riparian forest	<10 m	0
13	Isar (near Arzbach)	660	Large, isolated gravel banks; coarse substrate with sludge; relicts of riparian forest; algal growth; below Sylvenstein Reservoir (regulation of discharge)	10–50 m	2 (ee, r)
14	Lech (near Langweid)	440	Old riverbed of Lech River; riverbed only partly filled with slow running water; large gravel banks; coarse substrate and sludge; algal growth; main water flow redirected above this section	51–100 m	2 (ee)

Table 1: Characterisation of sampled river sections. Human impact: 0=natural condition, 1=minor human impact, 2=major human impact, e=embankment (ee=on both sides), w=weir upstream, r=reservoir upstream.

	Arzbach	Halblech	Hornbach	Iller near Rubi	Iller near Sonthofen	Isar near Arzbach	Isar near Schröfeln	Isar near Vorderriss	Lech near Forchach	Lech near Langweid	Ostrach	Schwarzenbach	Stillach	Streimbach
Nesticidae														
Nesticus cellulanus (Clerck, 1757)	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Theridiidae														
Robertus neglectus (O.P.-Cambr., 1871)	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Theridion varians Hahn, 1833	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Linyphiidae														
Araeoncus humilis (Blackwall, 1841)	—	—	—	—	—	—	—	—	—	1	—	—	1	—
Bathyphantes gracilis (Blackwall, 1841)	—	1	—	—	—	—	—	—	—	1	—	—	—	—
Bathyphantes nigrinus (Westring, 1851)	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Caviphantes saxetorum (Hull, 1916)	—	1	—	—	—	—	1	—	—	—	—	—	—	—
Centromerus incilium (L. Koch, 1881)	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Centromerus sylvaticus (Blackwall, 1841)	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Ceratinopsis romana (O.P.-Cambr., 1872)	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Diplocephalus cristatus (Blackwall, 1833)	—	1	2	1	—	1	—	—	—	—	—	—	—	—
Diplocephalus latifons (O.P.-Cambr., 1863)	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Erigone atra Blackwall, 1833	—	2	4	2	1	2	—	2	1	7	1	—	—	—
Erigone dentipalpis (Wider, 1834)	—	—	3	2	—	2	1	—	2	3	—	—	—	—
Gnathonarium dentatum (Wider, 1834)	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Janetschekia monodon (O.P.-Cambr., 1872)	—	—	1	—	—	—	1	—	4	—	1	1	2	1
Lepthyphantes pulcher (Kulczyński, 1881)	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Meioneta rurestris (C. L. Koch, 1836)	—	—	—	—	—	—	—	1	—	1	—	—	—	—
Oedothorax agrestis (Blackwall, 1853)	14	37	26	4	—	3	2	—	—	—	12	24	18	—
Oedothorax apicatus (Blackwall, 1850)	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Oedothorax retusus (Westring, 1851)	—	3	—	1	—	—	1	2	—	—	1	—	1	1
Porrhomma convexum (Westring, 1851)	—	—	2	1	—	—	—	—	—	—	—	2	—	—
Prinerigone vagans (Audouin, 1826)	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Tiso vagans (Blackwall, 1834)	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Araneidae														
Araneus diadematus Clerck, 1757	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Araniella opisthographa (Kulczyński, 1905)	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Lycosidae														
Arctosa cinerea (Fabricius, 1777)	—	—	—	—	—	—	4	3	1	—	—	—	—	—
Arctosa maculata (Hahn, 1822)	—	—	—	—	—	—	—	—	—	—	—	2	—	—
Pardosa amentata (Clerck, 1757)	—	1	—	—	—	—	—	—	—	—	—	—	5	—
Pardosa riparia (C. L. Koch, 1833)	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Pardosa saturatior Simon, 1937	—	—	2	—	—	—	—	—	—	—	—	—	5	3
Pardosa wagleri (Hahn, 1822)	27	—	1	4	5	1	2	16	11	—	36	8	—	2
Pirata knorri (Scopoli, 1763)	2	4	—	1	—	—	2	—	—	—	3	62	4	2
Trochosa ruricola (De Geer, 1778)	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Agelenidae														
Histopona torpida (C. L. Koch, 1834)	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Cybaeidae														
Cybaeus tetricus (C. L. Koch, 1839)	—	—	1	—	—	—	—	—	—	—	—	2	—	—
Hahniidae														
Cryphoeca silvicola (C. L Koch, 1834)	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Amaurobiidae														
Coelotes terrestris (Wider, 1834)	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Liocranidae														
Agraecina striata (Kulczyński, 1882)	1	—	—	—	—	1	—	—	—	—	1	1	—	1
Clubionidae														
Clubiona neglecta O.P.-Cambr., 1862	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Clubiona similis L. Koch, 1867	—	—	2	—	—	1	—	—	1	—	—	3	—	—
Clubiona trivialis C. L. Koch, 1843	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Gnaphosidae														
Zelotes latreillei (Simon, 1878)	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Zelotes subterraneus (C. L. Koch, 1833)	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Thomisidae														
Diaea dorsata (Fabricius, 1777)	—	—	—	—	—	—	—	1	—	—	—	—	—	—

Table 2: Numbers of adult spiders collected on the 14 investigated river sections in the northern parts of the European Alps. Nomenclature follows Platnick (1998).

species can also be found in dry, urban habitats (Maurer & Hänggi, 1990). *Arctosa cinerea* has been recorded from disused open brown coal mines (Hussein, 1998). Other non-riparian records for this species include gravel pits and sandy and pebble beaches of the North and Baltic Seas (Framenau, 1995).

The wolf spider *Pirata piraticus* is predominantly found in river and stream sections with reduced water velocity. Its typical habitats are the shores of lakes with a more or less dense cover of vegetation (Renner, 1986).

Species of open areas

Thirty-three (55%) of the species listed as "common or dominant" on river shores are generally known from open areas with a low cover of herbaceous vegetation. In the floodplains of larger rivers, these habitats are frequently found on the lower terraces which are only occasionally submerged (e.g. Moor, 1958; Müller & Bürger, 1990). Here, the soil moisture can vary considerably within a short distance depending on the water carrying capacity and the drainage quality of the soil. The "common or dominant" open land species were categorised by their preference for different degrees of humidity: xerophilous, mesophilic (hydrophilous) and indifferent species.

Six species (10%) prefer open, very dry habitats (xerophilous species). These areas are found particularly in the lower floodplains of gravel bed rivers and are often characterised by gravelly and stony soil surfaces with rather sparse vegetation cover. The category of mesophilic (hydrophilous) species comprises the largest number of species (21; 35%). Species in this group prefer intermediate to moist areas, which are typically covered by dense grass (Poaceae and Cyperaceae). Spiders of the genus *Oedothorax* are particularly common, with *Oedothorax retusus* being dominant on numerous river banks. Plachter (1986) recorded *Oedothorax fuscus* in unusually large numbers; a misidentification of the females appears to be likely, since the sibling species *O. agrestis* is commoner throughout all the other considered studies (cf. Růžička, 1978). A further six species (10%) do not prefer any specific substratum, moisture or vegetation cover but can be found in all types of open areas (indifferent open land species).

Forest-dwelling species

Eight species (13%) occur mainly in forests and similarly shaded habitats. Forest-dwelling species occur regularly on banks of small streams where the adjacent woodland reaches the banks and facilitates the invasion of these spiders.

Euryoecious species

Six species (10%) do not show any particular habitat preference and can therefore be characterised as generalists. *Erigone atra* and *E. dentipalpis* are among these species and occasionally attain high numbers on river banks.

The suitability of riparian spiders for indicating changes in floodplain dynamics

In the European Alps, gravel bank spider communities appear to be dominated by a few riparian specialists. Except for *Pirata piraticus*, all the species that we classified as stenoecious riparian are restricted to vegetation-free gravel banks. The reduction in number and size of gravel banks due to human interference might therefore be expected to result in a decline in the number of riparian species and their densities. Thus, riparian spiders have the potential to be used as indicators by comparing their diversity and density in disturbed and undisturbed river systems.

Arthropods, and in particular spiders, have commonly been suggested as ecological indicators (Clausen, 1986; Helsdingen, 1991; Kremen *et al.*, 1993; Platen, 1993; Malt, 1995; Neet, 1996; Churchill, 1998). The development of indicator systems requires the clear definition of (a) what environmental impact or change is

River	*Oedothorax agrestis*	*Pardosa wagleri*	*Pirata knorri*	*Pardosa saturatior*	All species
Hornbach	**1.44 ± 4.31**	0.06 ± 0.24		**0.11 ± 0.32**	2.5 ± 4.72
Streimbach		0.11 ± 0.47	0.11 ± 0.32	**0.17 ± 0.38**	0.78 ± 1
Lech (near Forchach)		**0.61 ± 0.98**			1.11 ± 1.18
Stillach	1 ± 2.64		**0.22 ± 0.55**	**0.28 ± 0.67**	2 ± 4.33
Ostrach	0.67 ± 1.41	2 ± 3.27	0.17 ± 0.51		3.06 ± 4.53
Isar (near Schröfeln)	0.11 ± 0.32	0.11 ± 0.32	0.11 ± 0.47		0.89 ± 1.41
Halblech	**2.06 ± 5.41**		**0.22 ± 0.43**		2.78 ± 5.94
Iller (near Rubi)	0.22 ± 0.55	0.22 ± 0.43	0.06 ± 0.24		1.17 ± 1.34
Isar (near Vorderriss)		**0.89 ± 2.11**			1.72 ± 3.27
Schwarzenbach	1.33 ± 2	0.44 ± 1.04	**3.44 ± 6.48**		6 ± 7.91
Iller (near Sonthofen)	0 ± 0	0.28 ± 0.96			0.33 ± 0.97
Arzbach	**0.78 ± 1.67**	**1.5 ± 3.67**	0.11 ± 0.32		2.44 ± 4.99
Isar (near Arzbach)	0.25 ± 0.62	0.08 ± 0.29			1.08 ± 2.28
Lech (near Langweid)					2.5 ± 1.05

Table 3: Mean (± s.e.) number of adult spiders (stenoecious riparian species and all encountered species) per 20 min sample ($n=18$ samples per river section, except Isar near Arzbach, $n=12$, and Lech near Langweid, $n=6$). Numbers in bold type represent the three highest values for each species.

	River section (Reference)	Hornbach (a)	Lech Vorderhornb./Häselg. (b)	Lech Forchach — Stanzach (b)	Lech near Forchach (a)	Stillach (a)	Streimbach (a)	Elmau (c)	Linder (c)	Upper Halblech (d)	Lech Höfen — Weissenbach (b)	Ostrach (a)	Neidernach 1 (c)	Lech Pflach — Lechaschau (b)	Lech Musau — Pinswang (b)	Neidernach 2 (c)	Isar near Schröfeln (a)	Isar near Vorderriss II (e)	Isar near Vorderriss I (a)	Isar near Vorderriss III (c)	Iller near Rubi (a)	Halblech (a)	Schwarzenbach (a)
		High-montane								**Montane**													
	Altitude (m) a.s.l.	1000	980	930	910	900	980	970	820–1010	890	860	860	850	840	820	820	810	780	770	770	770	770	760
Riparian species	*Pardosa saturatior* Simon, 1937	4	8	—	—	14	21	10	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(a)	*Pardosa wagleri* (Hahn, 1822)	2	1	5	55	—	14	—	—	23	6	65	8	1	6	6	13	28	52	19	19	—	7
	Oedothorax agrestis (Blackwall, 1853)	58	1	—	—	50	—	5	16	12	1	22	8	7	+	—	13	—	—	4	19	74	22
	Pirata knorri (Scopoli, 1763)	—	16	1	—	11	14	57	68	22	3	5	56	4	+	18	13	16	—	48	5	8	57
	Janetschekia monodon (O.P.-Cambr., 1872)	2	1	5	20	6	7	—	—	3	3	2	—	1	6	—	6	—	—	—	—	—	1
	Clubiona similis L. Koch, 1867	4	3	3	5	—	—	—	—	3	4	—	—	2	9	—	—	—	—	—	—	—	3
(b)	*Arctosa cinerea* (Fabricius, 1777)	—	—	+	5	—	—	—	—	—	1	—	—	—	—	—	25	11	10	11	—	—	—
	Caviphantes saxetorum (Hull, 1916)	—	—	2	—	—	—	—	—	1	6	—	—	1	2	—	6	—	—	—	—	2	—
	Diplocentria mediocris (Simon, 1884)	—	—	5	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—
(c)	*Pirata piraticus* (Clerck, 1757)	—	—	—	—	—	—	—	—	—	—	—	—	1	+	—	—	—	—	—	—	—	—
Species of open areas	*Pardosa torrentum* Simon, 1876	—	2	11	—	—	—	—	—	3	4	—	—	+	7	—	—	—	—	—	—	—	—
	Phrurolithus festivus (C. L. Koch, 1835)	—	+	—	—	—	—	—	—	+	1	—	—	—	—	—	—	—	—	—	—	—	—
xerophilous	*Drassyllus pumilus* (C. L. Koch, 1839)	—	+	1	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—
	Heliophanus patagiatus Thorell, 1875	—	—	+	—	—	—	—	—	3	—	—	—	—	5	—	—	—	—	—	—	—	—
	Phrurolithus minimus C. L. Koch, 1839	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Myrmarachne formicaria (De Geer, 1778)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Oedothorax retusus (Westring, 1851)	—	24	15	—	3	7	—	—	3	26	2	—	32	10	6	6	16	6	7	5	6	—
	Oedothorax fuscus (Blackwall, 1834)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	15	—	—	—	—	—
	Pardosa amentata (Clerck, 1757)	—	1	1	—	14	—	—	—	3	2	—	—	10	2	—	—	—	—	—	—	2	—
	Agraecina striata (Kulczyński, 1882)	—	1	—	—	—	7	—	—	1	1	2	—	+	1	—	—	—	—	—	—	—	1
	Oedothorax apicatus (Blackwall, 1850)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—
	Porrhomma convexum (Westring, 1851)	4	1	+	—	—	—	—	—	3	—	—	—	1	1	—	—	—	—	—	5	—	2
	Bathyphantes nigrinus (Westring, 1851)	—	—	—	—	—	—	—	—	+	—	—	—	—	0	—	—	—	—	—	5	—	—
	Bathyphantes gracilis (Blackwall, 1841)	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	2	—
	Trochosa ruricola (De Geer, 1778)	—	—	+	—	—	—	—	—	—	—	—	—	—	1	—	6	—	—	4	—	—	—
mesophilic	*Collinsia distincta* (Simon, 1884)	—	—	—	—	—	—	—	—	—	—	—	—	1	+	—	—	1	—	—	—	—	—
(hydrophilous)	*Pachygnatha clercki* Sundevall, 1823	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
	Trochosa terricola Thorell, 1856	—	—	—	—	—	—	—	—	1	—	—	8	0	—	—	—	—	—	—	—	—	—
	Oedothorax gibbosus (Blackwall, 1841)	—	—	—	—	—	—	—	—	—	—	—	—	2	+	—	—	—	—	—	—	—	—
	Pirata hygrophilus (Thorell, 1872)	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
	Pirata latitans Blackwall, 1833	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—
	Antistea elegans (Blackwall, 1841)	—	1	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
	Porrhomma pygmaeum (Blackwall, 1834)	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Pelecopsis mengei (Simon, 1884)	—	—	—	—	—	—	—	—	—	1	—	—	5	1	—	—	—	—	—	—	—	—
	Tiso vagans (Blackwall, 1834)	—	—	+	—	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Hypomma bituberculatum (Wider, 1834)	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—
	Prinerigone vagans (Audouin, 1826)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Diplocephalus cristatus (Blackwall, 1833)	4	8	1	—	—	—	5	—	1	1	—	—	4	3	—	—	—	—	—	5	2	—
	Meioneta rurestris (C. L. Koch, 1836)	—	—	0	—	—	—	—	2	2	1	—	—	—	2	6	—	1	3	4	—	—	—
indifferent	*Araeoncus humilis* (Blackwall, 1841)	—	+	1	—	3	—	—	—	+	1	—	—	—	—	—	—	—	—	—	—	—	—
	Micaria pulicaria (Sundevall, 1832)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Theridion varians Hahn, 1833	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Zelotes latreillei (Simon, 1878)	—	—	—	—	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Euryoecious species	*Erigone atra* (Blackwall, 1841)	9	3	15	5	—	—	10	—	1	5	2	4	3	5	35	—	—	6	—	10	4	—
	Erigone dentipalpis (Wider, 1834)	7	3	9	10	—	—	—	—	1	3	—	4	4	9	12	6	—	—	4	10	—	—
	Zelotes subterraneus (C. L. Koch, 1833)	—	+	+	—	—	—	—	2	1	—	—	—	—	+	—	—	—	—	—	—	—	1
	Araniella cucurbitina (Clerck, 1757)	—	+	1	—	—	—	—	—	+	—	—	—	+	+	—	—	—	—	—	—	—	—
	Pardosa lugubris (Walckenaer, 1802)	—	2	+	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
	Clubiona trivialis C. L. Koch, 1843	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	6	—	—	—	—	—	—
Forest-dwelling species	*Diplocephalus latifrons* (O.P.-Cambr., 1863)	—	+	+	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	10	—	—
	Centromerus sylvaticus (Blackwall, 1841)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Lepthyphantes tenebricola (Wider, 1834)	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
	Coelotes terrestris (Wider, 1834)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—
	Robertus neglectus (O.P.-Cambr., 1871)	—	—	+	—	—	7	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
	Diaea dorsata (Fabricius, 1777)	—	+	—	—	—	—	—	—	—	—	—	8	—	—	—	—	—	3	—	—	—	—
	Diplostyla concolor (Wider, 1834)	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—
	Philodromus collinus C. L. Koch, 1835	—	—	+	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—	—	—	—
?	*Leptorhoptrum robustum* (Westring, 1851)	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—
	Lessertinella kulczynskii (Lessert, 1909)	—	1	2	—	—	—	—	—	—	8	—	—	+	7	—	—	—	—	—	—	—	—
	Lepthyphantes pulcher (Kulczyński, 1881)	—	—	—	—	—	7	—	—	—	—	—	—	—	—	6	—	—	—	—	—	—	—
	% other species:	4	20	21	0	0	0	14	4	14	19	0	4	16	22	0	0	8	19	0	5	0	6
	total number of individuals:	*45*	*208*	*242*	*20*	*36*	*14*	*21*	*50*	*503*	*144*	*55*	*25*	*338*	*315*	*17*	*16*	*74*	*31*	*27*	*21*	*50*	*108*

Table 4: Dominance (%) of the ''common or dominant'' spider species of riparian gravel banks in Central Europe. Nomenclature follows Platnick (1998). ''+''=0–0.5. Riparian species: a=species with strong affinity to running water, b=species with limited affinity to running water, c=species of lake shores. References: (a) this study, (b) Steinberger (1996), (c) Hering (1995), (d) Dröschmeister (1994), (e) Plachter (1986), (f) Smit (1997), (g) Heidt *et al.* (1998).

	Montane				Submontane																Colline					
	720	**700**	**660**	**650**	**588**	**540**	**290–464**	**430**	**410**	**257–520**	**320–485**	**300–455**	**212–440**	**440**	**475**	**518**	**367/380**	**359**	**320**	**440**	**200**	**160**	**238–255**	**253–300**	**172–295**	**245**
	Iller near Sonthofen (a)	**Arzbach (a)**	**Isar near Arzbach (a)**	**Isar south Bad Tölz (e)**	**Isdar south Puppling (e)**	**Isar north Grünwalder Brücke (e)**	**Linspher Bach (f)**	**Isar south Marzling (e)**	**Isar near Volkmannsdorf (e)**	**Orke (f)**	**Perf (f)**	**Elbrighäuser Bach (f)**	**Treisbach (f)**	**Lech near Langweid II (e)**	**Isar nordwestl. Ismaning (e)**	**Isar München (e)**	**Isar near Niederaichbach (e)**	**Isar near Mamming (e)**	**Donau near Pondorf (e)**	**Lech near Langweid I (a)**	**Ain (g)**	**Tagliamento (g)**	**Lahn (f)**	**Eder (f)**	**Allna (f)**	**Rhône (g)**
Pardosa saturatior	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pardosa wagleri	83	61	8	43	30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	26	—	—	—	—
Oedothorax agrestis	—	32	23	—	—	—	69	—	—	63	13	79	80	2	—	—	—	—	—	—	14	—	23	1	79	—
Pirata knorri	—	5	—	14	13	7	14	2	8	15	25	5	5	28	—	—	—	—	—	—	—	—	9	18	—	—
Janestschekia monodon	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	—	—	—	—
Clubiona similis	—	—	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	3	—	—	—	—
Arctosa cinerea	—	—	—	4	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	—	—	—	—
Caviphantes saxetorum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diplocentria mediocris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
Pirata piraticus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—
Pardosa torrentum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phrurolithus festivus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	—	—	1	—	—	—	—	7
Drassyllus pumilus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—
Heliophanus patagiatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—
Phrurolithus minimus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	—	—	—	—	—
Myrmarachne formicaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—	—	—	—	—	—	—	—
Oedothorax retusus	—	—	—	4	18	61	5	33	6	6	—	3	—	1	—	40	9	—	43	—	2	3	22	49	2	—
Oedothorax fuscus	—	—	—	8	21	17	+	37	44	+	—	+	+	27	47	12	35	17	—	—	1	—	1	1	—	—
Pardosa amentata	—	—	—	4	—	—	2	—	—	1	8	+	—	2	25	5	—	—	5	—	1	—	11	2	—	—
Agraecina striata	—	2	8	6	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	6	7	—	—	—	7
Oedothorax apicatus	—	—	—	—	—	—	+	1	—	+	6	—	—	1	—	—	—	15	—	7	12	—	7	4	3	7
Porrhomma convexum	—	—	—	—	—	—	+	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Bathyphantes nigrinus	—	—	—	—	—	1	—	—	22	+	—	+	—	8	—	—	3	—	19	—	—	—	—	—	—	—
Bathyphantes gracilis	—	—	—	—	—	—	1	—	—	—	2	+	2	—	—	—	—	—	—	7	—	—	1	—	1	—
Trochosa ruricola	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	7	—	—	+	2	1	—	1	—
Collinsia distincta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28	5	—	—	5	—	1	—	4	—	—	—
Pachygnatha clercki	—	—	—	—	—	—	+	2	—	+	2	—	—	—	—	—	—	—	5	—	—	—	1	3	—	—
Trochosa terricola	—	—	—	—	—	—	+	—	—	—	2	—	—	—	—	—	—	—	—	—	+	—	1	—	—	—
Oedothorax gibbosus	—	—	—	—	—	—	1	—	—	—	2	+	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Pirata hygrophilus	—	—	—	—	—	—	+	—	—	+	2	2	—	—	—	—	—	—	—	—	—	—	—	—	2	—
Pirata latitans	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	2	—	—	—	—	18	1	—	—	—
Antistea elegans	—	—	—	—	—	—	+	—	—	—	—	—	+	—	—	—	—	—	—	—	1	—	—	—	—	—
Porrhomma pygmaeum	—	—	—	—	—	—	+	—	—	+	—	+	—	—	—	—	—	—	—	—	+	—	—	—	—	—
Pelecopsis mengei	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tiso vagans	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hypomma bituberculatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	—	—	—	—	—	—	—
Prinerigone vagans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	6	—	—	—	—	—
Diplocephalus cristatus	—	—	8	8	5	8	—	5	13	+	2	+	—	9	—	10	18	4	—	—	6	—	—	—	—	7
Meioneta rurestris	—	—	—	—	—	—	+	—	—	+	—	—	—	—	—	—	—	4	—	7	2	—	2	2	—	—
Araeoncus humilis	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	7	1	3	1	—	1	7
Micaria pulicaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—	—	—	1	—	—	—
Theridion varians	—	—	8	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Zelotes latreillei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Erigone atra	17	—	15	1	5	2	1	9	4	2	21	1	1	6	—	10	11	20	5	47	2	—	8	14	9	13
Erigone dentipalpis	—	—	15	—	2	3	1	2	1	2	4	0	1	5	—	19	—	15	—	20	5	3	3	2	2	33
Zelotes subterraneus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Araniella cucurbitina	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pardosa lugubris	—	—	—	—	—	—	—	2	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Clubiona trivialis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diplocephalus latifrons	—	—	—	—	—	—	—	—	—	+	2	0	4	—	—	—	—	—	—	—	—	—	—	—	—	—
Centromerus sylvaticus	—	—	8	—	—	—	+	—	—	+	4	1	+	1	—	—	—	—	—	—	—	—	—	—	—	—
Lepthyphantes tenebricola	—	—	—	—	—	—	+	—	—	+	—	+	+	—	—	—	2	—	—	—	—	—	—	—	—	—
Coelotes terrestris	—	—	—	—	—	1	+	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Robertus neglectus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaea dorsata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diplostyla concolor	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Philodromus collinus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptorhoptrum robustum	—	—	—	—	—	—	+	—	—	2	2	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—
Lessertinella kulczynskii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lepthyphantes pulcher	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	0	0	0	7	0	0	7	6	2	8	2	8	6	8	0	0	6	4	0	0	7	10	2	2	2	0
	6	*44*	*13*	*72*	*56*	*103*	*976*	*86*	*85*	*614*	*48*	*1142*	*342*	*96*	*36*	*42*	*66*	*46*	*21*	*15*	*362*	*61*	*176*	*97*	*126*	*15*

Table 4: Continued.

to be indicated, (b) what effect this change has on the indicator organism (e.g. morphological change, reduction in numbers), and (c) how this change can be accurately measured (New, 1995). The environmental impact of hydrological engineering can be easily established by comparing historic data of discharge patterns and river morphology with current information. However, the consequence of these changes on floodplain spider populations appears to be rather unclear and a methodology to determine differences is difficult to implement.

The restriction of *Pardosa saturatior* to rivers and streams above 800 m makes it exempt from human interference. *Pardosa wagleri* is predominantly found above an altitude of 500 m, also suggesting a geographically restricted distribution. Its presence below 200 m at the Ain and Tagliamento Rivers (Heidt *et al*., 1998) suggests that human impact may have a more important influence on its distribution than ecological preferences, since the impact of dams, weirs and embankments is more prominent in the lower catchment. However, *P. wagleri* does not seem to be affected by changes in the floodplain dynamics. It is abundant in floodplains with both minor (Lech near Forchach [910 m], Isar near Vorderriss [770 m]) and extensive human impacts (Iller near Sonthofen [720 m], Isar south of Bad Tölz [650 m]).Therefore, its use as an indicator species appears to be limited. *Oedothorax agrestis* and *Pirata knorri* are common not only on gravel banks in the European Alps but also by small streams in low mountainous areas both with and without human interference (Smit, 1997). There was no significant correlation between the intensity of human impact and abundance of these two species in our study.

It is difficult to establish a standardised sampling method to quantify potential differences in spider diversity and abundance between rivers with and without hydrological constructions. Pitfall traps near the river bank are very likely to be flooded, and hand samples are subject to variation depending on the individual investigator (Plachter, 1986; Dröschmeister, 1995). Differences in the abundance of gravel bank spiders might also be a consequence of differences in habitat structure, e.g. size composition of gravel. Our knowledge of habitat preferences for any of the riparian species is still inadequate to interpret any variation in spider densities.

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