1999. The Journal of Arachnology 27:222–228

SPIDER AND HARVESTMAN COMMUNITIES ALONG A GLACIATION TRANSECT IN THE ITALIAN DOLOMITES

Vito Zingerle: Institute of Zoology and Limnology, University of Innsbruck, Technikerstrasse 25, 6020 Innsbruck, Austria

ABSTRACT. Arachnid communities of alpine grassland, of screes and woodlands near the timberline and of the nival zone have been compared along a transect from the northern to the southern border of the Dolomites. The region is zoogeographically interesting because of differences of the ice cover during glaciation, which was less severe in the southern area. Along the whole transect spider communities in grasslands and at the timberline zone show approximately the same composition. Endemic species, e.g, *Harpactea grisea* (Canestrini 1868), *Amaurobius ruffoi* Thaler 1990, *Coelotes mediocris* Kulczynski 1887, *Cybaeus intermedius* Maurer 1992 and *Eudasylobus ligusticus* Roewer 1923 occur mostly on the southernmost station, which remained free of ice. Re-immigrants over short distance are scarce, e.g., *Coelotes mediocris* at Passo Rolle and *Coelotes solitarius* L. Koch 1868 in the Puez area. Endemic species were not found in the alpine grassland of the northern Dolomites, which suggests severe impact of glacial events on the local fauna. Central alpine species, i.e., *Erigonella subelevata* (L. Koch 1869), *Metopobactrus nadigi* Thaler 1976, *Meioneta orites* (Thorell 1875), *Pardosa blanda* (C.L. Koch 1833) and *Pardosa mixta* (Kulczynski 1887) are still present at the southernmost boundary of the Alps. Nunataks in the northern and central area of the Dolomites allowed speciation effects within the nival fauna: *Lepthyphantes brunneri* Thaler 1984, *Lepthyphantes merretti* Millidge 1974, *Megabunus armatus* (Kulczynski 1887). Further zoogeographically interesting records are *Cryphoeca nivalis* Schenkel 1919 and *Xysticus bonneti* Denis 1938.

RIASSUNTO. È stata studiata la composizione della fauna aracnologica della zona subalpina, alpina e nivale lungo un transetto che parte dalle Dolomti settentrionali (Parco Naturale Puez-Odle) e porta fino al bordo meridionale delle Alpi (Monte Grappa). Il versante meridionale delle Alpi è di grande importanza ai fini di studi zoogeografici, essendo queste regioni in parte rimaste libere dai ghiacciai durante le epoche glaciali. Sul Monte Grappa sono state riscontrate piú specie endemiche p.es. *Harpactea grisea* (Canestrini 1868), *Amaurobius ruffoi* Thaler 1990, *Coelotes mediocris* Kulczynski 1887, *Cybaeus intermedius* Maurer 1992 e *Eudasylobus ligusticus* Roewer 1923. Alcune specie reimmigranti a breve distanza hanno riconquistato parti delle Dolomiti raggiungendo regioni piú a nord: *Coelotes mediocris* Kulczynski 1887 è stato catturato anche a Passo Rolle, *Coelotes solitarius* L. Koch 1868 anche nel Parco Naturale Puez-Odle. Specie endemiche sembrano essere assenti nella prateria alpina delle Dolomiti settentrionali, dimostrando l'effetto distruttivo dei ghiacciai sulla fauna del suolo. In questa zona si possono trovare specie endemiche sulle cime piú alte rimaste libere dai ghiacciai: *Lepthyphantes merretti* Millidge 1974, *Lepthyphantes brunneri* Thaler 1984 e *Megabunus armatus* (Kulczynski 1887). Altre specie rare e di notevole interesse zoogeografico catturate nell'ambito di questo studio sono *Cryphoeca nivalis* Schenkel 1919 e *Xysticus bonneti* Denis 1938. È particolarmente sorprendente la presenza sul Monte Grappa di specie tipiche delle Alpi centrali che sembrano spingersi fino al bordo piú meridionale delle Alpi, p.es. *Erigonella subelevata* (L. Koch 1869), *Metopobactrus nadigi* Thaler 1976, *Meioneta orites* (Thorell 1875), *Pardosa blanda* (C.L. Koch 1833) e *Pardosa mixta* (Kulczynski 1887).

The southern Alps are interesting for zoogeographical research. During glaciation periods most of the Alps were covered with a thick ice layer (Klebelsberg 1935; Husen 1987), but ice-free conditions (massivs de refuge) along the southern and south-eastern border made survival of animal and plant species possible (Holdhaus 1954). A few species also survived on summits rising above the ice shield (nunataks, Janetschek 1956). Ice-free regions played an important part in differentiation of new species as well as in recolonization after glaciation. Therefore widely distributed faunal elements are present in the central Alps, whereas in the southern Alps also endemic species occur. Thaler (1976) recognized the main families which form endemic species on the southern border of the Alps: Dysderidae, Linyphiidae, Agelenidae and Amaurobiidae. Maurer (1982a) and Maurer &

Thaler (1988) studied living conditions in refugial areas and discussed the possible duration of speciation and migration.

Still little is known about spider communities living in the Dolomites. Koch (1876) and Kulczynski (1887) presented the first lists of the arachnids from this area. Further results concerning spiders or harvestmen of the Dolomite region were published by Janetschek (1957), Denis (1963) and Marcellino (1988). Marcuzzi (1956, 1975) provided general surveys of the fauna of the Dolomites. Noflatscher (1996) and Hellrigl (1996) summarized the spider and harvestman fauna of the South-Tyrol territory, including the northern part of the Dolomites. Lists of the spiders and harvestmen of northern Italy were given by Pesarini (1994) and Chemini (1994). Recently the spider fauna of the Puez region was studied by Zingerle (1997).

This paper compares arachnid communities from sites near the timberline, from alpine grasslands and from nival habitats along a transect between the northern Dolomites and the southern border of the Alps. It is part of the results of a larger study on the spider fauna of the Dolomites performed by the author.

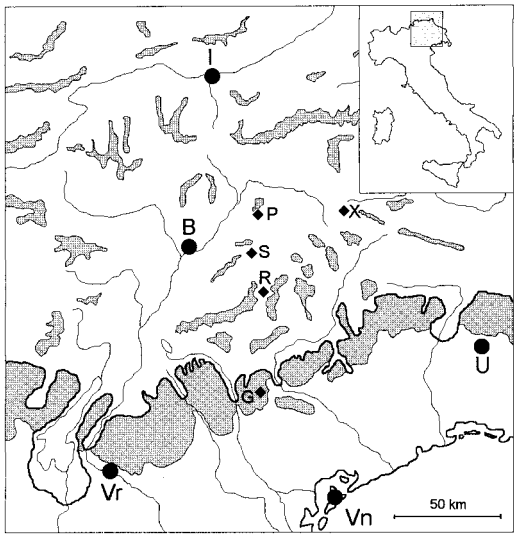

Figure 1.—Map showing position of the sampling areas in the Dolomites (Northern Italy) and ice-cover situation during glaciation (according to Klebelsberg 1935). Shaded area indicates ice-free regions on the border of the south-eastern Alps and nunataks (see text). Study sites: G = Monte Grappa (MG); P = Puez Nature Park (PU); S = Passo Sella (SE); R = Passo Rolle (RO); X = Sesto/Sexten Nature Park (SX). Main Cities in the vicinity of the study areas: B = Bolzano (Bozen); I = Innsbruck; U = Udine; Vn = Venice; Vr = Verona.

METHODS

Study sites.—The study sites are situated in the northeastern corner of Italy, about 60 (Monte Grappa) to 140 km (Puez Nature Park) north of Venice in the regions Veneto and Trentino-South Tyrol (Fig. 1). The Dolomite Mountains are mainly composed of limestone and dolomite rock. Several summits rise up to more than 3000 m, the highest elevation is Mount Marmolada with 3342 m. Different forest types can be found due to decreasing rainfall and mediterranean influence between the southern border of the Dolomites and the central Alps. In southern sites the timberline occurs at 1700 m elevation and rises continuously up to 2300 m towards the north. In the timberline zone of the southern Dolomites mostly spruce and beech forest (*Picea abies*, *Fagus sylvatica*) are found; in northern sites larch (*Larix decidua*), cembra-pine (*Pinus cembra*) and mountain pine (*Pinus mugo*) exist. Ditches and humid places are mostly covered by associations of *Alnus viridis* and of *Salix* spp. Alpine grasslands on limestone and dolomite rock are dominated by *Carex sempervirens* and *Sesleria albicans*. On bare rocks of the mountain tops there grow patches of mosses and grasses, like *Carex firma* and *Carex rupestris*. For a general view of the area, see Fig. 2. Five study areas were selected (see Fig. 1): *Monte Grappa*, elevation 1775 m, 45°55′N, 11°49′E, at the border between the Provinces Belluno, Vicenza and Treviso. *Passo Rolle*, Paneveggio Pale-S. Martino Nature Park, elevation 1970 m, 46°18′N, 11°48′E, Province Trento. *Passo Sella*, elevation 2244 m, 46°30′N, 11°48′E, at the border between Provinces Trento and South-Tyrol. *Puez Nature Park*, Antersasc Valley, elevation 2000 m, 46°37′N, 11°52′E, Province South-Tyrol. *Sesto/Sexten Nature Park*, Gsell area, elevation 2000 m, 46°40′N, 12°22′E, Province South-Tyrol.

Collection methods.—In each of the five study areas mentioned above, three habitats types (grassland, scree and forest at the timberline) were sampled by pitfall traps. Four covered traps containing a formalin/water solution and a small amount of detergent were

Figure 2.—Typical landscape of the Dolomites in the vicinity of Passo Rolle (RO). Alpine grasslands and subalpine woodlands sampled are visible on the left side of the photo, nival habitats on the right side.

placed a few meters apart from each other in each habitat. Altogether 15 sites were sampled by 60 traps. The traps remained in the area throughout a whole year and were emptied in intervals of 3–4 weeks during the vegetation period. In the Puez area sampling was carried out from Spring 1995 to Spring 1996, in the other areas from Spring 1997 to Spring 1998. For details about the traps see Zingerle (1997). The mean number of specimens per trap, number of species, diversity value (^{2}log) according to Shannon-Weaver and family composition are given for each site.

Additionally, alpine and nival habitats were sampled during Summer 1995, 1996 and 1997 by hand collecting. This sampling technique is effective, due to the low species number in these habitats. Hand collecting was performed at the following localities: Puez (2600–2900 m), Sella (2900–3150 m), Sasso Lungo (Langkofel) (2700 m), Passo Falzarego (2400 m), Tofana (2950–3220 m), Cristallo (2400–2950 m), Sesto/Sexten (2450 m), Marmolada (3000–3300 m) and Pale di S. Martino (2700–3000 m).

Voucher specimens will be deposited in the Natural History Museum, Vienna (Austria) and in Naturmuseum Südtirol, Bozen (Italy).

RESULTS

Spiders and harvestmen of alpine grasslands and timberline zone.—The total material captured by pitfalls comprises 3640 adult specimens from 164 species and 15 families. The dominant families are: Linyphiidae (41% of specimens), Lycosidae (39%), Agelenidae (5%) Gnaphosidae (5%), Thomisidae (5%). Characteristics of the spider fauna found at each site are shown in Table 1.

On the whole transect family composition of spiders in grassland sites is approximately the same. In grasslands Lycosidae reach 48–74% of the total spiders. The most dominant species are *Pardosa blanda* (C.L. Koch 1833), *Pardosa oreophila* Simon 1937, *Alopecosa taeniata* (C.L. Koch 1848), *Pardosa riparia* (C.L. Koch 1833), *Trochosa terricola* Thorell 1856 and *Pardosa ferruginea* (L. Koch 1870). Fluctuation of abundance among these species in different areas is probably coincidental. The high abundance of Lycosidae in alpine grassland habitats is a well-known phenomenon. The secondmost important family is Linyphiidae (14–49%), mostly species with a preference for sites with an open canopy cover and little shade, like *Centromerus pabulator* (O.P.-

Table 1.—Structure of spider communities studied with pitfall traps in the Dolomites (Southern Alps, Italy) from spring 1995 to spring 1998. Abbreviations: x = mean number of individuals; S = number of species; H′ = Shannon-Weaver diversity (^{2}log). Percentages = number of specimens from a specific family ÷ the total number of spiders captured in a habitat during the whole sampling period. Habitats: G = alpine grassland; S = scree; T = forest sites near the timberline. Study areas: MG = Monte Grappa; RO = Passo Rolle; SE = Passo Sella; PU = Puez Nature Park (see also Zingerle 1997); SX = Sesto/Sexten Nature Park.

Habitat			Study areas				
			MG	RO	SE	PU	SX
G	x		98	102	80	79	93
	S		40	27	32	24	24
	H′		3.6	3.3	2.2	2.7	3.1
	Family composition	Lycosidae %	67	63	74	65	48
		Linyphiidae %	20	14	18	19	49
		Gnaphosidae %	10	11	4	7	1
		Thomisidae %	1	11	1	7	0
		others %	2 (4 fam.)	1 (4 fam.)	3 (5 fam.)	2 (4 fam.)	2 (5 fam.)
S	x		32	10	26	14	25
	S		30	9	16	15	16
	H′		4.2	2.4	2.9	3.5	3.0
	Family composition	Thomisidae %	2	44	31	30	46
		Linyphiidae %	24	39	42	24	23
		Lycosidae %	16	10	26	26	23
		Gnaphosidae %	29	2	0	9	0
		Dysderidae %	17	0	0	0	0
		Theridiidae %	0	0	0	7	1
		others %	12 (4 fam.)	5 (1 fam.)	1 (1 fam.)	4 (1 fam.)	7 (2 fam.)
T	x		35	65	37	115	99
	S		30	28	31	39	37
	H′		3.8	3.4	3.5	3.9	3.8
	Family composition	Linyphiidae %	75	75	46	55	76
		Lycosidae %	9	14	42	12	10
		Agelenidae %	9	4	1	29	2
		Gnaphosidae %	4	1	9	2	1
		Theridiidae %	0	5	0	1	6
		others %	3 (5 fam.)	1 (2 fam.)	2 (2 fam.)	1 (3 fam.)	5 (3 fam.)

Cambridge 1875), *Tiso vagans* (Blackwall 1834) and *Bolyphantes alticeps* (Sundevall 1832). High numbers of Linyphiidae (e.g., in Sesto) occur in the proximity of a dense vegetation cover. Shannon-Weaver diversity in grasslands reaches values between 2.2 and 3.6. The harvestman *Eudasylobus ligusticus* Roewer 1923, endemic to the southern border of the Alps, occurs in grasslands on Monte Grappa. The absence of an endemic *Coelotes* species in my collection in grasslands of this area is quite interesting (Maurer 1982a, b).

Screes are generally characterized by lower numbers of individuals and species. High diversity values (e.g., Monte Grappa) are found, when the influence of adjacent habitats is great. So the dominant thomisid species (*Xysticus lanio* C.L. Koch 1824, *Xysticus desidiosus* Simon 1875 and *Xysticus audax* (Schrank 1803)) also occur in grassland areas. Typical inhabitants of alpine screes are *Lepthyphantes variabilis* Kulczynski 1887, *Tiso aestivus* (L. Koch 1872), *Rugathodes bellicosus* Simon 1873 and *Pardosa nigra* (C.L. Koch 1834). In screes on Monte Grappa exist also endemic spiders, *Harpactea grisea* (Canestrini 1868) and *Amaurobius ruffoi* Thaler 1990, and the endemic harvestman *Eudasylobus ligusticus*. All these are invaders from the neighboring forests.

Forests near the timberline are dominated by linyphiid spiders, which reach 46–76% of

Table 2.—Presence (+) or absence (−) of zoogeographically interesting spider and harvestman species in alpine grassland and woodlands near the timberline collected by pitfall traps in the Dolomites (Southern Alps, Italy) from Spring 1995 to Spring 1998. Study areas: PU = Puez Nature Park; SX = Sesto/Sexten Nature Park; SE = Passo Sella; RO = Passo Rolle; MG = Monte Grappa.

Species	Study areas				
	PU	SX	SE	RO	MG
Harpactea grisea (Canestrini 1868)	−	−	−	−	+
Amaurobius ruffoi Thaler 1990	−	−	−	−	+
Cybaeus intermedius Maurer 1992	−	−	−	−	+
Eudasylobus ligusticus Roewer 1923	−	−	−	−	+
Coelotes mediocris Kulczynski 1887	−	−	−	+	+
Coelotes solitarius L. Koch 1868	+	−	−	+	−
Metopobactrus nadigi Thaler 1976	+	−	+	−	+
Meioneta orites (Thorell 1875)	+	−	+	−	+
Pardosa blanda (C.L. Koch 1833)	+	−	+	−	+
Lepthyphantes cf. *fragilis* (Thorell 1875)	+	+	+	+	−
Troglohyphantes tirolensis Schenkel 1950	+	+	+	+	−
Pardosa mixta (Kulczynski 1887)	+	−	+	+	+
Erigonella subelevata (L. Koch 1869)	+	+	+	+	+

the spiders collected there. In addition, a high abundance of Agelenidae was found. Timberline sites are interesting because at this ecotone species from forest and alpine habitats occur together. Accordingly Lycosidae are also quite numerous and amount to 42% of all individuals from these habitats. Species numbers are generally higher than in other habitats and the Shannon-Weaver diversity index reaches values between 3.4 and 3.9, indicating a ''mixed'' fauna. Typical and abundant species from forest sites, which occur in the timberline zone are *C. pabulator*, *Diplocephalus latifrons* (O. P.-Cambridge 1863), *Lepthyphantes monticola* (Kulczynski 1882), *Lepthyphantes jacksonoides* Helsdingen 1977, *Cybaeus tetricus* (C.L. Koch 1839) and *Cryphoeca silvicola* (C.L. Koch 1834); species from alpine grassland are *P. blanda*, *A. taeniata*, *P. oreophila* and *P. riparia*. Endemic spiders and harvestmen collected on Monte Grappa are: *Amaurobius ruffoi*, *Coelotes mediocris* Kulczynski 1887, *Cybaeus intermedius* Maurer 1992 and *Eudasylobus ligusticus*. Remarkable is the occurrence of *C. mediocris* at timberline sites of Passo Rolle.

Hand catches in alpine and nival zones.—Spider and harvestman communities in these zones are mainly composed of few specialists which, however, occur abundantly. Thaler (1981, 1988) collected 27 spider species in the nival zone of the central Alps and 49 nival species on 58 summits of the eastern Alps. In the present study a total of 29 spider (299 individuals) and 4 harvestman species (11 individuals) were collected on 16 summits of the Dolomites between 2400–3300 m elevation. Twenty-two of these species belong to Linyphiidae, 2 to Theridiidae, 2 to Thomisidae, 1 to Agelenidae, Lycosidae and Philodromidae, respectively. Several of these species collected in high numbers on most summits show a rather continuous distribution in the studied area. Only two of them, *Hilaira montigena* (L. Koch 1873) and *Erigone tirolensis* (L. Koch 1872), occur mainly in the nival zone, the rest, (e.g., *L. variabilis*, *Meioneta gulosa* (L. Koch, 1869), *Diplocephalus helleri* (L. Koch 1869) and *Oreonetides glacialis* (L. Koch 1872)) are also present in the alpine zone. The ballooning lowland species *Meioneta rurestris* (C.L. Koch 1836) also occurs frequently in the nival zone. The harvestmen (*Dicranopalpus gasteinensis* Doleschall 1852, *Mitopus glacialis* (Heer 1845) and *Megabunus armatus* (Kulczynski 1887)) occur in the nival and in the alpine zone, whereas *Ischyropsalis kollari* C.L. Koch 1839 is also present in the montane woodland. Furthermore, two endemic spider species (i.e., *Lepthyphantes merretti* Millidge 1974 and *L. brunneri* Thaler 1984) with a mainly nival distribution were found quite numerously at certain localities (see Table 3). The endemic harvestman *Megabunus armatus* was also collected several times. These species demonstrate that the highest

Table 3.—Presence (+) or absence (−) of zoogeographically interesting spider and harvestman species in the alpine zone and the nival zone of the Dolomites (Southern Alps, Italy) collected by hand during Summer 1995, 1996 and 1997. Sampled localities: SE = Sella; PU = Puez; MA = Marmolada; PA = Pale di S. Martino; PF = Passo Falzarego; SL = Sasso Lungo/Langkofel; TO = Tofane; SX = Sesto/Sexten; CR = Cristallo.

Species	Sampled localities								
	SE	PU	MA	PA	PF	SL	TO	SX	CR
Lepthyphantes merretti Millidge 1974	+	+	+	+	−	−	−	−	−
Lepthyphantes brunneri Thaler 1984	−	−	−	−	−	−	+	+	+
Megabunus armatus (Kulczynski 1887)	+	+	−	−	+	+	+	−	−
Cryphoeca nivalis Schenkel 1919	−	−	−	+	−	−	−	−	−
Xysticus bonneti Denis 1938	−	−	−	−	+	−	−	−	−

summits of the Dolomites were spared by glaciation events, allowing speciation to take place. Two remarkable nival spiders species were captured only at one site each: *Cryphoeca nivalis* Schenkel 1919 on Pale di S. Martino (2700 m) and *Xysticus bonneti* Denis 1938 in the vicinity of Passo Falzarego (2400 m).

DISCUSSION

The fauna of spiders and harvestman from the alpine and the timberline zone of the Dolomites shows a similar composition in the northern and in the southern area. Nevertheless, a few species indicate a minor impact of glaciation events in the border region and give evidence for peripheral isolation in the southern Dolomites (e.g., *Harpactea grisea, Amaurobius ruffoi, Cybaeus intermedius, Coelotes mediocris* and *Eudasylobus ligusticus*). Whether these species occur at northern sites or not depends on their capabilities to re-colonize the area after glaciation (see Table 2). Some species, like *H. grisea, A. ruffoi, C. intermedius* and *E. ligusticus*, seem to be restricted to the southernmost border, occurring exclusively on Monte Grappa. Others, (e.g., *Coelotes mediocris*), re-immigrated into the area up to Passo Rolle and show a higher mobility. *Coelotes solitarius* probably survived glaciation periods near the south-eastern border of the Alps; nevertheless it was found all the way up to the northernmost site, the Puez area. Populations of *Lepthyphantes* cf. *fragilis* (Thorell 1875) and *Troglohyphantes tirolensis* Schenkel 1950 were also influenced by glaciation, but further taxonomic work is needed to realize their precise status. Maurer (1982a, b) reported the occurrence of 10 species of the *Coelotes pastor*-group from alpine grasslands between Liguria (Italy) and Slovenia, e.g., *C. pastor lessinensis* Maurer 1982 on Monti Lessini and *Coelotes alpinus* Polenec 1972 in the eastermost area. Species from this group were not found during this study. Remarkable is the presence of central-alpine spiders, (i.e., *Erigonella subelevata, Metopobactrus nadigi, Meioneta orites, Pardosa blanda* and *P. mixta*) at the southermost limit of the Alps at Monte Grappa.

The nival fauna of the Dolomites demonstrates isolation effects and speciation on nunataks during glaciations. The endemic Linyphiidae *Lepthyphantes merretti* and *L. brunneri* were found on only a few summits, *L. brunneri* being distributed in the eastern and *L. merretti* in the western area of the Dolomites (see Table 3; Thaler 1988). The endemic harvestman *Megabunus armatus* is restricted to the south-eastern Alps where it lives on rocks above the timberline. The vicariance pattern in this genus in the Alps probably reflects the effects of glaciation (Martens 1978; Chemini 1985). The agelenid *Cryphoeca nivalis* was previously known only from the Adamello and Brenta area in Italy and from the central Swiss Alps (Thaler 1978; Maurer & Hänggi 1990). The station in the Dolomites is probably close to its eastermost boundary of distribution. *Xysticus bonneti* is a rarely found species (Thaler 1981), which shows a very patchy distribution in the alpine zone of the western palearctic mountains.

ACKNOWLEDGEMENTS

I thank Dr. Konrad Thaler for help with species identifications, discussion and manuscript review. For suggestions I am also grate-

ful to Dr. Peter Schwendinger. The following institutions provided equipment, support and permits: Institute of Zoology, University of Innsbruck (Austria); Museo Scienze Naturali Alto Adige, Bolzano/Naturmuseum Südtirol, Bozen (Italy); Ufficio Parchi Naturali, Bolzano/Amt für Naturparke, Bozen (Italy); Ente Parco Paneveggio - Pale di S. Martino (Italy).

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Manuscript received 29 April 1998, revised 6 September 1998.