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Diversity and ecology of spider assemblages of a Mediterranean wetland complex

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Abstract. Wetland complexes in Mediterranean deltas play an important ecological role, as they harbor a diverse flora and fauna with numerous specialized species. Intensification and expansion of agricultural land use, as well as increasing withdrawal of water over the past decades, has led to considerable habitat loss in many places. Although studies from temperate Europe have already demonstrated the conservation needs of wetlands, analogous data for the Mediterranean region are very scarce. The present paper analyzes spider assemblages of the Aladjagiola wetland complex and provides ecological descriptions of diversity patterns and assemblage structures. We aim to provide the first ecological descriptions of several species and effective data sets to characterize the ecological status of the wetland habitats investigated. Spiders were collected by pitfall trapping from April to July 2008 in seven habitat types: pseudo-maquis, dry grassland (short growth), dry grassland (long growth), fringes, reed belts, humid grassland and fallow land. Diversity (alpha and functional) and evenness were both found to be lowest in humid habitat types. Community structure was analyzed by non-metric multidimensional scaling. Humid habitat types harbored a distinct species assemblage comprising many hygrophilic species that could clearly be separated from all other habitat types. By means of generalized linear models, habitat preferences of numerous xerophlic, hygrophilic and photophilic species could be assessed. Our study demonstrated that especially humid habitat types are worth protecting.

Keywords: Aladjagiola wetland complex, Araneae, east Macedonian-Thracian wetland belt, functional diversity, Greece, Nestos Delta

Mediterranean deltas comprise a broad variety of habitat types (Hecker & Vives 1995). Among them, coastal dunes and lagoons with salt marshes, as well as fresh-water habitats such as dynamic riparian gravel and sand banks, alluvial forests, lakes and adjacent wetlands play an important ecological role, as they harbor a diverse flora and fauna including numerous specialized species (Krcmar & Merdic 2007; Buchholz 2009). Most Mediterranean deltas have been heavily impacted by anthropogenic measures (e.g., drainage, water storage, salinization, grazing and pisciculture) and are thus highly endangered (Britton & Crivelli 1993).

The Aladjagiola wetland complex is located in northeast Greece within the Nestos Delta, forming the westernmost part of the east Macedonian and Thracian wetland belt. Although covering a relatively small area (approximately 20 km^2), previous studies have consistently indicated high species richness within numerous taxonomic groups (amphibians and reptiles: Donth 1996; butterflies: Schumann 1996; spiders: Schröder et al. 2011). Despite their ecological relevance, the wetlands of the Aladjagiola have been subjected to a continuous intensification and expansion of agricultural land use over the past decades. Together with an increasing withdrawal of water, this has led to considerable habitat loss in the whole region (Mallinis et al. 2011). Currently, the conversion of land and the alteration in water supply of the Nestos River are an immediate threat, which has led to an increasing desiccation of freshwaters and the adjacent wetland habitat types.

Invertebrates such as spiders are generally suitable early warning organisms and bioindicators. By studying invertebrate communities it is possible to assess the conservation value of certain habitat types, and several authors claim a more prominent consideration for conservation and biodiversity studies (Finch & Niedringhaus 2010). In this context, analyzing assemblages and species-environment relationships can provide valuable data bases for nature conservation policies and habitat management guidelines (Buchholz 2010; Cristofoli et al. 2010). Spiders have proven to be a suitable model group within a broad variety of ecological studies (Buchholz 2010; Schirmel et al. 2012) as they are abundant and species-rich, easy to sample and show distinct spatial and temporal habitat preferences (Entling et al. 2007; Schirmel & Buchholz 2011). To date, ecological analyses of spider assemblages of eastern Mediterranean ecosystems are very scarce, and thus information on ecology and habitat preferences of many spider species is mostly missing.

This paper analyzes spider assemblages of the Aladjagiola wetland complex. Apart from ecological descriptions of diversity patterns and assemblage structures, this work aims to provide effective data sets to characterize the ecological status of the investigated habitat types that could be used within the framework of conservation and both ecological planning and management. Authorities for scientific names appear in Appendix I.

STUDY AREA

Aladjagiola is part of the Nestos Delta and is located in East Macedonia, in northeast Greece, between 41°00′ and 41°02′N, and between 24°40′ and 24°44′E. It comprises an area of approximately 20 km^2 (Mattes & Lienau 1996) (Fig. 1). The northern border of the Nestos Delta directly adjoins the southernmost part of the Rhodope Mountains. The study area is located northeast of the city of Chrysoupolis. The climate is Mediterranean with 600–700 mm annual precipitation and 16° C annual average temperature (Lienau 1989).

Within the study area, dry habitats, mainly represented by patches of dry calcareous grassland within scattered pseudo-maquis formations, as well as fresh water lakes with adjacent

Figure 1.—Location of the Aladjagiola wetland complex in the western part of the Nestos Delta, in northeast Greece.

reed banks and humid meadows, form a diverse habitat mosaic. Habitat heterogeneity is additionally enhanced by diverse small-scale vegetation elements within the agricultural landscape, especially fringes and hedges along irrigation canals and arable fields. The biggest lake, Megali Limni, is thought to be a former lagoon that lost its connection to the sea during the delta developing process. Lakes and ponds in the western part of the study site are of anthropogenic origin as a result of intensive clay and sand mining, while standing water bodies near the Nestos River are assumed to have emerged from former oxbows of the Nestos River (Jerrentrup et al. 1989).

METHODS

Sampling.—Spiders were collected by pitfall trapping from April to July 2008. Pitfall traps measured 9 cm in diameter and were filled with a 4% formalin/detergent solution. The position of each trap (three traps per sampling site) was randomly determined, but minimum distance between traps was 5 m. Traps were emptied fortnightly. The investigations were conducted in seven main habitat types (pseudo-maquis, dry grassland – short growth and long growth, fringes, reed beds, humid grassland, fallow land), each with three replicates, resulting in a total of 21 sampling sites and 63 pitfall traps. For habitat description three environmental parameters were assessed once at the end of May (Table 1). Vegetation structure [cover of herb layer (%)] was estimated in an area of 1 m^2 around each pitfall trap. The three measurements per sampling site were afterwards averaged. According to AG Boden (1994), soil humidity was estimated in the field and categorized into five classes: 1 = dry, 2 = slightly humid, 3 = humid, 4 = very humid and 5 = wet. Shading was estimated as percentage of canopy openness and assigned to five shading classes: 1 = no shading (0–20%), 2 = low shading (20–40%), 3 = moderate shading (40–60%), 4 = high shading (60–80%) and 5 = very high shading (80–100%).

Analysis.—Alpha diversity (number of species, Shannon diversity, Shannon evenness) was expressed as the number of species at each site. Shannon diversity and Shannon evenness were calculated using PAST (Hammer et al. 2001).

Although species richness is usually the simplest and most intuitive measure for diversity within the framework of biodiversity and conservation studies, the use of functional diversity, which integrates information on life-history traits, has grown rapidly in recent years in ecological research (e.g., Violle et al. 2007), since the realization that life-history traits play an important role in diversity (Vandewalle et al. 2010). Functional diversity concepts can provide a useful approach to integrate biodiversity research into the broader context of ecosystem processes and functioning, and recently Schirmel et al. (2012) demonstrated that functional diversity of spiders is more sensitive than alpha diversity and therefore contributes valuable information for conservation.

Three functional diversity indices were calculated using the R environment package FD: functional dispersion (FDis), functional evenness (FEve) and functional divergence (FDiv) (Villéger et al. 2008; Laliberté & Legendre 2010). FDis is a measure of functional richness, which considers species relative abundances by estimating their dispersion in a multidimensional trait space. In the following, we interpret functional dispersion as a measure for functional diversity per se. FEve combines both the evenness of trait distribution and the evenness of species relative abundances. The index is 1 if all species have equal abundance and if all the traits are evenly distributed in trait space, and it declines toward zero with

Table 1.—Environmental characteristics of the sampled habitat types. Explanations – classes for soil humidity (soil.hum): 1 = dry, 2 = slightly humid, 3 = humid, 4 = very humid, 5 = wet; classes of shading (measured as canopy openness): 1 = no shading, 2 = low shading, 3 = moderate shading, 4 = high shading, 5 = very high shading; cov.veg = vegetation cover.

habitat type	no. of sites	soil.hum	shading	cov.veg [%]
pseudo-maquis [PM]	3	2	4	75
dry grassland – short growth [DGs]	3	1	1	70
dry grassland – long growth [DGl]	3	2	2	95
fringes [FR]	3	2	3	80
reed belts [RE]	3	5	2	80
humid grassland [HG]	3	4	2	90
fallow land [FL]	3	2	1	70

Table 2.—Spider diversity of habitat types pseudo-maquis (PM), dry grassland – short growth (DGs), dry grassland – long growth (DGl), fringes (FR), reed belts (RE), humid grassland (HG) and fallow land (FL). Alpha diversity is expressed as number of species (number of species), Shannon-Index and Shannon-Evenness (mean ± SEM). For functional diversity, functional dispersion (FDis), functional evenness (FEve) and functional divergence (FDiv) were calculated (mean ± SEM). Differences among habitat types were tested using one-way ANOVA (significance levels: *** $P < 0.001$, ** $P > 0.01$, n.s. = not significant). Pairwise comparisons were done using the Holm-Sidak test, and different letters indicate significant differences between groups at $P < 0.05$.

	habitat types							
	PM	DGs	DGl	FR	RE	HG	FL	*F*
alpha diversity								
no. species	26 ± 3	42 ± 3	40 ± 4	43 ± 2	34 ± 9	40 ± 11	24 ± 2	1.9$^{n.s.}$
Shannon	2.59 ± 0.20^{a}	3.22 ± 0.03^{b}	3.02 ± 0.10^{b}	2.84 ± 0.19$^{a, b, d}$	2.11 ± 0.18^{c}	2.63 ± 0.15^{d}	2.56 ± 0.06$^{a, b, d}$	6.8***
Evenness	0.51 ± 0.06^{a}	0.61 ± 0.04^{a}	0.52 ± 0.05^{a}	0.42 ± 0.07$^{a, b}$	0.26 ± 0.02^{b}	0.40 ± 0.08$^{a, b}$	0.54 ± 0.03^{a}	4.6**
functional diversity								
FDis	0.38 ± 0.01^{a}	0.36 ± 0.01^{a}	0.38 ± 0.01^{a}	0.34 ± 0.05^{a}	0.26 ± 0.03^{b}	0.24 ± 0.01^{b}	0.40 ± 0.02^{a}	7.1***
FEve	0.71 ± 0.03^{a}	0.71 ± 0.02^{a}	0.69 ± 0.01^{a}	0.71 ± 0.02^{a}	0.59 ± 0.04^{b}	0.60 ± 0.01^{b}	0.72 ± 0.03^{a}	5.2**
FDiv	0.84 ± 0.01	0.79 ± 0.01	0.83 ± 0.03	0.90 ± 0.02	0.89 ± 0.03	0.86 ± 0.03	0.85 ± 0.04	1.8$^{n.s.}$

increasing unevenness in either aspect. Lastly, FDiv expresses the distance of the most abundant species from the centroid of the assemblage in trait space. FDiv is high when the most abundant species have extreme trait values. It can be interpreted as a measure of variance (Laliberté & Legendre 2010).

To calculate functional diversity, spiders were first assigned to life history trait categories with the help of literature data (Appendix I). The following traits were analyzed: body size, hunting mode and ballooning. Hunting and ballooning were coded categorically according to Cardoso et al. (2011) (ambush hunters, ground hunters, other hunters, orb web, sensing web, sheet web, space web, specialists) and Bell et al. (2005) (ballooning uncommon = genus not listed as ballooners in Bell et al. 2005, less common = genus listed, common = species listed). For body size (total body length), metric data (mm) were taken for females from Nentwig et al. (2013).

For multivariate analyses, only dominant species occurring with frequencies of more than 3.1% per site were taken from the dataset of Schröder et al. (2011). Omitting rare species is an appropriate method to reduce statistical noise in the data set without losing much information. In order to analyze spider species assemblages, a non-metric multidimensional scaling (NMDS) using VEGAN and MASS packages was applied. Prior to the analyses, relative abundances of each species were square root transformed. The NMDS was based on the Bray-Curtis dissimilarity matrix of spiders. In search of a stable solution, a maximum of 100 random starts was used. After seven tries, two convergent solutions were found for a three -dimensional model. A permutational multivariate analysis of variance (MANOVA based on 10,000 permutations) was performed to assess the impact of habitat type and of soil humidity (as an analogue for habitat humidity) on species abundance distribution and assemblage separation.

Poisson generalized linear models (GLM) were applied to test the effects of environmental constraints (predictor variables: soil humidity, shading, vegetation cover) on species that occurred with more than nine individuals. To compensate for overdispersion, standard errors were corrected using a quasi-Poisson model. The residual deviance was used as a goodness-of-fit measure by calculating the pseudo R^2 (Zuur et al. 2009).

All statistical analyses were performed with R 3.0.1 (R Core Team 2013).

RESULTS

Significant differences among habitat types could be detected for Shannon diversity and evenness (ANOVA, $F = 6.8$, $P = 0.001$; $F = 4.6$, $P = 0.007$), although differences in species numbers were not significant (Table 2). Species assemblages of reed belts were less diverse (Shannon = 2.11) than those of all other habitat types. Accordingly, evenness was lowest in reed belts (0.26). Functional diversity also differed significantly among habitat types (Table 2). Functional dispersion and functional evenness were lowest in humid habitat types (FDis = 0.26 and 0.24 for reed belts and humid grassland, respectively, ANOVA, $F = 7.1$, $P = 0.001$; FEve = 0.59 and 0.60, ANOVA, $F = 5.2$, $P = 0.004$). Higher values were calculated for dry habitat types.

In total, 43 species out of 2,208 individuals were submitted to a multivariate analysis. The stress value for a three-dimensional NMDS was 7.92. The scaling plot illustrated two distant habitat groups comprising clearly distinct spider species assemblages (Fig. 2). Humid habitat types (reed, humid grassland) (on the right) were separated from more or less dry habitats on the left. Most abundant in humid habitat types were several lycosid species such as *Arctosa leopardus*, *A. tbilisiensis*, *Aulonia kratochvili*, *Pardosa paludicola*, *P. prativaga*, *P. vittata*, *Pirata latitans* and *Trochosa ruricola* as well as *Oedothorax apicatus*. Dry habitats were separated from pseudo-maquis, where *Brachythele denieri*, *Harpactea babori* and *Scytodes thoracica* were typical species. Dry grassland and fallow land sites harbored a similar species assemblage comprising numerous gnaphosid and salticid species; e.g., *Callilepis cretica*, *Gnaphosa lucifuga*, *Nomisia exornata*, *N. ripariensis*, *Pellenes diagonalis*, *P. nigrociliatus*, *Phlegra fasciata*, *Trachyzelotes barbatus*, *T. lyonneti* and *Zelotes tenuis*.

Soil humdity contributed significantly to species grouping, as indicated by the permutational multivariate analysis of variance ($F = 8.1$, $P < 0.001$, $R^2 = 0.29$, 10,000 permutations). Accordingly, generalized linear models showed that most species responded significantly to soil humidity (Table 3). Activity densities of wetland species such as *Arctosa leopardus*,

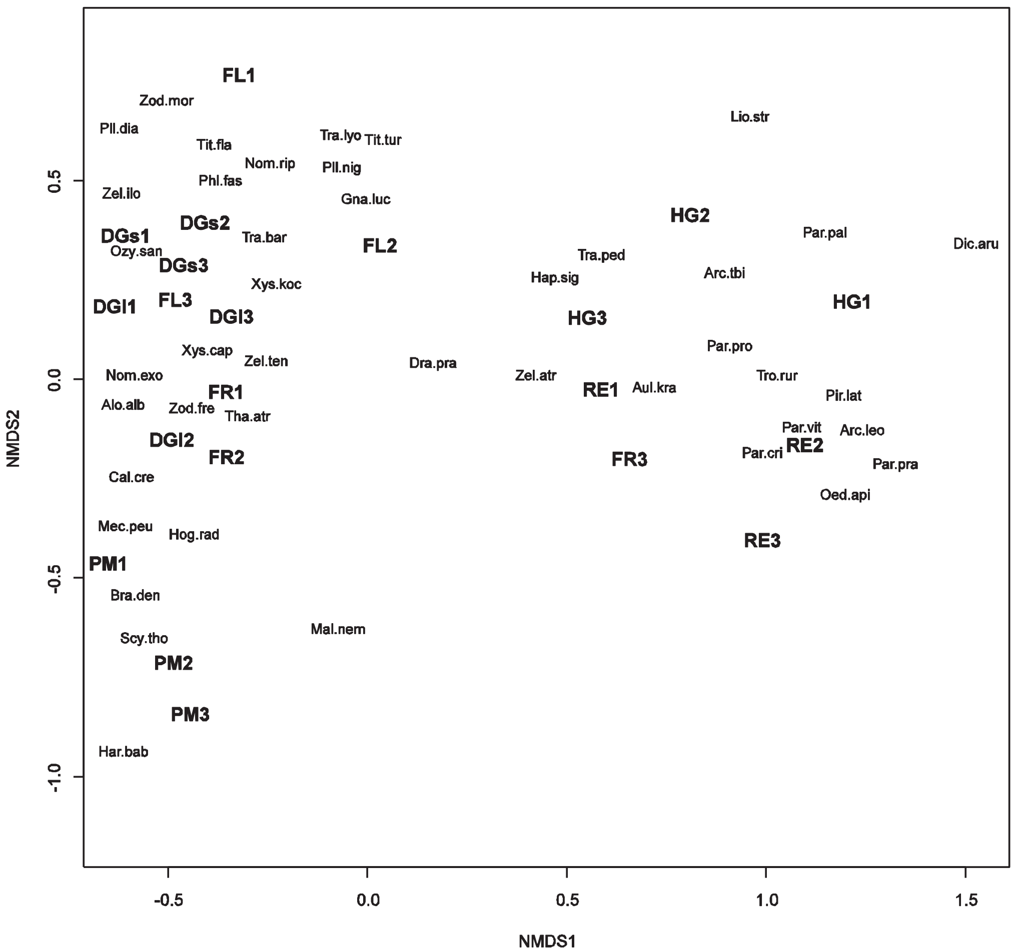

Figure 2.—NMDS plot based on spider densities (stress = 7.92, three dimensions). Habitat type significantly affected compositional differences of assemblages (permutational multivariate analysis of variance, $F = 3.3$, $P < 0.001$, $R^2 = 0.69$, 10,000 permutations). Abbreviations—sites: PM1–3 = pseudo-maquis, DGs1–3 = dry grassland, short growth, DGl1–3 = dry grassland, long growth, FR1–3 = fringes, RE1–3 = reed beds, HG1–3 = humid grassland, FL1–3 = fallow land; —species: Alo.alb = *Alopecosa albofasciata*, Arc.leo = *Arctosa leopardus*, Arc.tbi = *Arctosa tbilisiensis*, Aul.kra = *Aulonia kratochvili*, Bra.den = *Brachythele denieri*, Cal.cre = *Callilepis cretica*, Dic.aru = *Dictyna arundinacea*, Dra.pra = *Drassyllus praeficus*, Gna.luc = *Gnaphosa lucifuga*, Hap.sig = *Haplodrassus signifer*, Har.bab = *Harpactea babori*, Hog.rad = *Hogna radiata*, Lio.str = *Liocranoeca striata*, Mal.nem = *Malthonica nemorosa*, Mec.peu = *Mecophistes peusi*, Nom.exo = *Nomisia exornata*, Nom.rip = *Nomisia ripariensis*, Oed.api = *Oedothorax apicatus*, Ozy.san = *Ozyptila* cf. *sanctuaria*, Par.cri = *Pardosa cribrata*, Par.pal = *Pardosa paludicola*, Par.pra = *Pardosa prativaga*, Par.pro = *Pardosa proxima*, Par.vit = *Pardosa vittata*, Pll.dia = *Pellenes diagonalis*, Pll.nig = *Pellenes nigrociliatus*, Phl.fas = *Phlegra fasciata*, Pir.lat = *Pirata latitans*, Scy.tho = *Scytodes thoracica*, Tha.atr = *Thanatus atratus*, Tit.fla = *Titanoeca flavicoma*, Tit.tur = *Titanoeca turkmenia*, Tra.bar = *Trachyzelotes barbatus*, Tra.lyo = *Trachyzelotes lyonneti*, Tra.ped = *Trachyzelotes pedestris*, Tro.rur = *Trochosa ruricola*, Xys.cap = *Xysticus caperatus*, Xys.koc = *Xysticus kochi*, Zel.atr = *Zelotes atrocaeruleus*, Zel.ilo = *Zelotes ilotarum*, Zel.ten = *Zelotes tenuis*, Zod.fre = *Zodarion frenatum*, Zod.mor = *Zodarion morosum*.

Aulonia kratochvili, *Pardosa vittata*, *Pirata latitans* and *Trochosa ruricola* increased with increasing soil humidity, while those of xerophilic species (e.g., *Harpactea babori*, *Nomisia exornata*, *Xysticus caperatus*) decreased. Other environmental parameters were less influential, as only a few species were affected by either shading or vegetation cover. Of these, *Pellenes diagonalis* and *Xysticus kochi* responded negatively to increasing shading, while activity densities of *Brachythele denieri* increased.

DISCUSSION

Studies from Central Europe have demonstrated the importance of wetlands for the conservation of spider diversity (e.g., Weiss et al. 1998; Holec 2000), and Greenwood et al. (1995) showed that species diversity was higher in wetland habitats than in arable land. For the Mediterranean region analogous data are scarce, apart from very few studies that have assessed the conservation importance of reed beds (Schmidt et al. 2005) and freshwater habitats such as floodplains, river shores and humid grasslands (Buchholz 2009).

Spider assemblages of reed belts were less diverse than those of all other habitat types and showed lower evenness values, which indicate higher habitat dynamics and disturbance effects (Kratochwil & Schwabe 2001). This is most likely related to temporal flooding, and it appears that humid habitat types are inhabited by a few specialized species. These show high abundances (e.g., *Arctosa leopardus*: $n = 554$; *A. tbilisiensis*: $n = 245$) and are able to cope with disturbance due

Table 3.—Responses of spider species to selected environmental variables analyzed by GLM. Whether or not the variable had a positive or negative effect on species activity densities is indicated by "−" for decreasing (negative) and "+" for increasing (positive) effect. Significance levels are indicated as ***($P < 0.001$), **($P < 0.01$) or *($P < 0.05$). Abbreviated environmental predictor variables: soil.hum = soil humidity, cov.veg = vegetation cover. For a complete species list from Aladjagiola see Schröder et al. (2011). Only species with significant response are shown.

species	individuals	soil.hum	shading	cov.veg	R^2
Alopecosa albofasciata	79	− **	.	+ *	52.5
Arctosa leopardus	238	+ **	.	.	66.6
Arctosa tbilisiensis	110	+ *	.	.	76.8
Aulonia kratochvili	139	+ **	.	.	41.9
Brachythele denieri	11	.	+ *	.	44.2
Callilepis cretica	68	− *	.	.	32.6
Drassyllus praeficus	39	+ *	.	.	17.4
Haplodrassus signifer	32	+ *	.	.	41.8
Harpactea babori	16	− **	+ ***	.	76.6
Mecophistes peusi	10	.	.	− *	38.0
Nomisia exornata	21	− **	.	− *	70.8
Oedothorax apicatus	170	+ *	− *	.	66.5
Pardosa paludicola	52	+ *	.	.	83.2
Pardosa prativaga	182	+ *	.	.	45.1
Pardosa proxima	145	+ *	.	+ **	84.1
Pardosa vittata	61	+ ***	− ***	.	89.4
Pellenes diagonalis	18	.	− *	.	80.4
Pirata latitans	71	+ **	.	.	59.1
Scytodes thoracica	33	− *	.	.	75.4
Thanatus atratus	81	− **	.	+ *	45.0
Trachyzelotes pedestris	18	+ *	.	.	50.6
Trochosa ruricola	173	+ ***	.	.	78.9
Xysticus caperatus	51	− **	.	+ *	43.2
Xysticus kochi	42	.	− *	.	32.5
Zodarion frenatum	15	− *	.	.	37.0
Zodarion morosum	11	− *	− **	+ *	61.3

to flooding. Accordingly, functional evenness was lowest in reed belts as well as in humid grasslands. Although flooding was less common in humid grasslands than in reed belts, disturbance and habitat dynamics still affected species assemblages. With regard to functional evenness, lower values do not only indicate high habitat dynamics and disturbance effects, but also a less balanced niche occupancy (Schleuter et al. 2010) caused by the occurrence of rigorously hygrophilic species that occupy the same ecological niches. According to Villéger et al. (2008) both functional and species richness are closely related, and thus it is not surprising that humid sites had a lower functional diversity. In general, low functional diversity values can be explained by a lower number of available niches (Schirmel et al. 2012), which results from very homogeneous reed belts that provide only a minimally diverse habitat structure.

Conservation importance of wetland habitats.—Humid sites harbored numerous hyrophilic species (e.g., *Arctosa leopardus*, *A. tbilisiensis*, *Aulonia kratochvili*, *Oedothorax apicatus*, *Pardosa paludicola*, *P. prativaga*, *P. vittata*, *Pirata latitans* and *Trochosa ruricola*). Species assemblages could be clearly separated from those of dry habitats that included mostly xerophilic and photophilic species such as *Brachythele denieri*, *Harpactea babori*, *Nomisia exornata*, *Pellenes diagonalis*, *Scytodes thoracica*, *Xysticus caperatus* and *X. kochi*. A number of studies from Central Europe have shown that wetlands harbor unique spider assemblages that show a high sensitivity to altered soil humidity conditions (Bell et al. 1999; Bonn et al. 2002). However, due to lower precipitation and higher mean temperatures during the summer, effects on spider assemblages as well as activity levels might be much stronger in the Mediterranean region than in the temperate climate zone of Central and Northern Europe. Thus, the intensity of the anthropogenic impacts on the hydrological regime might be even more serious. In the case of the Aladjagiola wetland this would be crucial, since water withdrawal and consequent drying-out of freshwaters and adjacent wetland habitat types is highest by far during the summer (Taubert 1996).

Our study demonstrates that especially humid habitat types that suffer an ongoing habitat loss are worth protecting, as they harbor a unique spider assemblage. Analyses also showed that numerous species were constrained by soil humidity. These rigorously hygrophilic species depend strongly on the occurrence of wetland habitat types. Thus, it is likely that with proceeding habitat loss, the wetland assemblages will disappear. In addition, hygrophilic species may decline or, if it comes to the worst, they may even become extinct. Data for conservation issues—including ecological descriptions—are mostly rare in the eastern Mediterranean region. This is a drawback since updated datasets are urgently needed to, firstly, assess the conservation status of certain habitat types and, secondly, provide a basis for nature conservation strategies and habitat management objectives. Therefore, our results have particular importance for the northeastern Greek wetlands, which belong to a region that is of nationwide conservation importance due to its landscape diversity and biogeographical uniqueness (e.g., Jerrentrup et al. 1989;

Schröder et al. 2011). Considering the ongoing habitat loss and degradation, preservation and restoration of the remaining wetland habitats is urgently needed. We showed the importance of using spiders as a model group, knowing that spider species are an adequate surrogate for the conservation value of the total invertebrate fauna (Scott et al. 2006). On the other hand, data from Aladjagiola suggest that conservation importance does not only apply to invertebrates (e.g., Schumann 1996) but also to higher taxa (Donth 1996). Thus, there is an urgent need to drastically reduce the water withdrawal and to develop a more sustainable irrigation regime. Furthermore, land conversion planning must ensure the highest possible habitat diversity by conserving wetland habitats and thus preserving their unique spider assemblages.

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Appendix I.—Individual number of spiders and life-history traits [according to Bell et al. 2005 (ballooning), Cardoso et al. 2011 (hunting), Nentwig et al. 2013 (female body size' mm)]. PM = pseudo-maquis, DGs = dry grassland – short growth, DGl = dry grassland – long growth, FR = fringes, RE = reed belts, HG = humid grassland, FL = fallow land.

	Life-history traits			Abundances							
Species	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Agelenidae											
Agelena orientalis C.L. Koch 1837	13.50	sheet web	less common	3	2	3	1	.	.	.	9
Malthonica nemorosa (Simon 1916)	10.75	sheet web	uncommon	8	.	1	9	.	2	.	20
Tegenaria angustipalpis Levy 1996	5.90	sheet web	uncommon	.	.	.	1	.	.	.	1
Amaurobidae											
Amaurobius erberi (Keyserling 1863)	9.50	sheet web	uncommon	1	.	.	1	.	.	.	2
Araneidae											
Agalenatea redii (Scopoli 1763)	7.50	orb web	uncommon	.	.	1	.	.	1	.	2
Araneus angulatus Clerck 1757	17.00	orb web	less common	.	1	.	.	.	.	.	1
Cercidia prominens (Westring 1851)	6.00	orb web	uncommon	.	.	.	.	.	1	.	1
Cyrtarachne ixodoides (Simon 1870)	6.70	orb web	uncommon	.	.	.	.	1	.	.	1
Gibberanea bituberculata (Walckenaer 1802)	9.00	orb web	uncommon	.	.	1	5				6
G. gibbosa (Walckenaer 1802)	7.50	orb web	uncommon	1	.	.	.	.	.	.	1
Hypsosinga albovittata (Westring 1851)	4.00	orb web	common	.	1	2	.	.	.	1	4
Larinioides cornutus (Clerck 1757)	11.75	orb web	common	.	.	1	.	.	.	.	1
Mangora acalypha (Walckenaer 1802)	5.75	orb web	common	1	.	1	1	.	.	.	3
Neoscona adianta (Walckenaer 1802)	6.25	orb web	less common	.	.	1	5	.	1	1	8
Zilla diodia (Walckenaer 1802)	4.00	orb web	uncommon	1	.	.	.	.	.	.	1
Atypidae											
Atypus piceus (Sulzer 1776)	12.50	sensing web	uncommon	.	.	1	.	.	.	.	1
Clubionidae											
Clubiona lutescens Westring 1851	7.00	other hunters	less common	.	.	.	.	1	.	.	1
C. phragmitis C.L. Koch 1843	9.50	other hunters	less common	.	.	.	1	.	.	.	1
Corinnidae											
Phrurolithus festivus (C.L. Koch 1835)	3.00	ground hunters	uncommon	3	2	2	10	2	3	.	22
P. szilyi Herman 1879	2.50	ground hunters	uncommon	3	1	1	1	.	.	.	6
Dictynidae											
Archaeodictyna consecuta (O.P.-Cambridge 1872)	2.00	space web	uncommon	1	.	.	.	1	.	.	2
Dictyna arundinacea (Linnaeus 1758)	3.25	space web	common	.	.	.	.	.	9	.	9
Dysderidae											
Dysdera longirostris Doblika 1853	7.00	specialists	uncommon	1	.	.	5	.	4	.	10
Harpactea babori (Nosek 1905)	7.60	specialists	uncommon	27	1	1	14	.	.	.	43
Stalagtia thaleriana Chatzaki & Arnedo 2006	5.50	specialists	uncommon	.	1	.	.	.	.	.	1
Eresidae											
Eresus kollari Rossi 1846	12.50	sheet web	uncommon	2	2	5	.	2	.	.	11
Filistatidae											
Pritha nana (Simon 1868)	3.45	sensing web	uncommon	5	1	.	.	.	.	.	6
Gnaphosidae											
Aphantaulax cincta (L. Koch 1866)	6.00	ground hunters	uncommon	.	1	.	.	.	.	.	1
A. trifasciata (O.P.-Cambridge 1872)	5.50	ground hunters	uncommon	.	.	.	1	.	.	.	1

APPENDIX—Continued.

	Life-history traits			Abundances							
Species	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Callilepis cretica (Roewer 1928)	5.50	ground hunters	uncommon	36	32	54	66	.	1	.	189
Camillina metellus (Roewer 1928)	4.00	ground hunters	uncommon	.	.	.	.	.	.	2	2
Drassodes lapidosus (Walckenaer 1802)	12.00	ground hunters	uncommon	.	1	5	1	1	1	3	12
D. pubescens (Thorell 1856)	7.50	ground hunters	uncommon	.	1	.	1	3	2	.	7
Drassyllus lutetianus (L. Koch 1866)	5.00	ground hunters	common	.	.	.	.	2	1	1	4
D. praeficus (L. Koch 1866)	6.00	ground hunters	common	2	13	6	24	15	36	6	102
Gnaphosa lucifuga (Walckenaer 1802)	15.50	ground hunters	less common	.	.	.	6	1	1	32	40
Haplodrassus dalmatensis (L. Koch 1866)	6.00	ground hunters	uncommon	.	2	5	2	.	.	5	14
H. invalidus (O.P.-Cambridge 1872)	7.50	ground hunters	uncommon	.	1	.	.	.	.	.	1
H. minor (O.P.-Cambridge 1879)	3.50	ground hunters	uncommon	.	.	.	1	.	14	.	15
H. signifer (C.L. Koch 1839)	8.50	ground hunters	uncommon	.	11	6	14	6	37	4	78
Micaria albovittata (Lucas 1846)	6.25	ground hunters	common	.	.	.	.	2	14	1	17
M. coarctata (Lucas 1846)	5.40	ground hunters	common	.	.	.	1	.	.	.	1
M. guttulata (C.L. Koch 1839)	2.95	ground hunters	common	1	3	5	1	.	.	.	10
M. pulicaria (Sundevall 1831)	3.50	ground hunters	common	.	.	.	2	7	5	.	14
Nomisia exornata (C.L. Koch 1839)	6.00	ground hunters	uncommon	4	37	11	7	.	.	.	59
N. ripariensis (O.P.-Cambridge 1872)	7.30	ground hunters	uncommon	.	19	5	5	.	4	8	41
Trachyzelotes barbatus (L. Koch 1866)	8.30	ground hunters	common	.	7	7	4	.	4	.	22
T. lyonneti (Audouin 1826)	7.10	ground hunters	common	.	1	.	7	.	7	2	17
T. malkini Platnick & Murphy 1984	6.95	ground hunters	common	.	.	1	1	.	2	2	6
T. pedestris (C.L. Koch 1837)	7.50	ground hunters	common	.	.	3	4	2	32	.	41
Zelotes argoliensis (C.L. Koch 1839)	6.35	ground hunters	common	.	1	.	4	.	.	.	5
Z. atrocaeruleus (Simon 1878)	7.00	ground hunters	common	.	2	1	16	10	33	.	62
Z. caucasius (L. Koch 1866)	5.50	ground hunters	common	.	1	1	.	.	.	1	3
Z. gracilis (Canestrini 1868)	2.00	ground hunters	common	.	.	.	1	.	.	.	1
Z. ilotarum (Simon 1884)	7.45	ground hunters	common	3	11	2	.	.	.	1	17
Z. longipes (L. Koch 1866)	6.00	ground hunters	common	.	.	1	1	.	2	1	5
Z. segrex (Simon 1878)	5.10	ground hunters	common	.	12	6	1	.	.	.	19
Z. tenuis L. Koch 1866	6.55	ground hunters	common	3	6	6	3	.	3	.	21
Hahniidae											
Antistea elegans (Blackwall 1841)	3.00	sheet web	uncommon	.	.	.	.	1	5	.	6
Linyphiidae											
Acartauchenius scurrilis (O.P.-Cambridge 1872)	1.85	other hunters	uncommon	.	.	1	.	.	.	3	4
Ceratinella brevipes (Westring 1851)	1.70	other hunters	less common	1	.	.	.	2	.	.	3
C. brevis (Wider 1834)	2.00	other hunters	less common	1	.	.	.	1	2	.	4
Diplostyla concolor (Wider 1834)	2.75	sheet web	common	.	.	.	.	.	15	.	15
Enteclara acuminata (Wider 1834)	2.20	other hunters	less common	1	.	.	.	.	.	.	1
Erigone dentipalpis (Wider 1834)	2.30	other hunters	common	1	2	.	.	2	1	1	7
Frontinellina frutetorum (C.L. Koch 1834)	5.50	sheet web	less common	.	.	1	.	.	.	.	1
Gnathonarium dentatum (Wider 1834)	2.40	other hunters	common	.	2	.	.	16	.	.	18
Gongylidiellum murcidum Simon 1884	1.60	other hunters	common	1	.	.	.	.	.	.	1
Gongylidium rufipes (Linnaeus 1758)	3.40	other hunters	uncommon	.	.	.	2	.	.	.	2
Mecophistes peusi Wunderlich 1972	1.60	other hunters	uncommon	11	15	3	1	.	.	.	30
Meioneta fuscipalpa (C.L. Koch 1836)	1.90	sheet web	less common	.	.	.	.	.	.	1	1
M. pseudorurestris (Wunderlich 1980)	1.80	sheet web	less common	.	.	1	.	2	2	2	7
Neriene clathrata (Sundevall 1830)	4.35	sheet web	common	1	.	.	1	.	.	.	2
Oedothorax apicatus (Blackwall 1850)	2.75	other hunters	common	.	8	.	2	389	5	.	404
Pelecopsis elongata (Wider 1834)	2.05	other hunters	common	.	.	.	.	1	.	.	1
P. parallela (Wider 1834)	1.65	other hunters	common	1	1	.	.	.	.	6	8
Pocadicnemis juncea Locket & Millidge 1953	1.90	other hunters	uncommon	.	.	.	.	2	2	.	4
Prinerigone vagans (Audouin 1826)	2.10	other hunters	common	.	1	.	.	17	2	.	20
Scutpelecopsis krausi (Wunderlich 1980)	1.40	other hunters	common	.	1	.	.	.	.	.	1
Syaedra gracilis (Menge 1869)	2.45	other hunters	uncommon	3	.	.	.	.	.	.	3
Trichoncus hackmani Millidge 1955	2.10	other hunters	uncommon	.	1	5	.	3	1	.	10
Walckenaeria alticeps (Denis 1952)	2.35	other hunters	common	2	.	.	3	.	.	.	5
W. vigilax (Blackwall 1853)	2.55	other hunters	common	.	.	.	.	3	.	.	3
Liocranidae											
Agraecina lineata (Simon 1878)	8.00	ground hunters	uncommon	.	.	1	.	.	1	.	2

Appendix—Continued.

	Life-history traits			Abundances							
Species	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Agroeca cuprea Menge 1873	4.00	ground hunters	uncommon	.	.	.	4	.	1	.	5
A. lusatica (L. Koch 1875)	6.00	ground hunters	uncommon	.	.	.	.	.	9	.	9
Liocranoeca striata (Kulczyn'ski 1882)	5.00	ground hunters	uncommon	.	.	.	.	.	38	.	38
Lycosidae											
Alopecosa albofasciata (Brullé 1832)	11.00	ground hunters	less common	58	16	14	51	5	2	31	177
A. pentheri (Nosek 1905)	9.00	ground hunters	less common	.	2	.	.	.	.	1	3
Arctosa leopardus (Sundevall 1833)	9.00	ground hunters	less common	.	.	.	3	411	143	.	557
A. perita (Latreille 1799)	7.75	ground hunters	common	.	.	.	1	8	1	4	14
A. tbilisiensis Mcheidze 1946	6.50	ground hunters	less common	.	.	.	3	28	217	2	250
Aulonia kratochvili Dunin, Buchar & Absolon 1986	5.00	ground hunters	less common	.	.	36	93	62	149	.	340
Geolycosa vultuosa (C.L. Koch 1838)	18.50	ground hunters	less common	.	2	1	.	.	.	.	3
Hogna radiata (Latreille 1817)	18.50	ground hunters	less common	11	4	12	4	1	.	1	33
Pardosa agrestis (Westring 1861)	7.50	ground hunters	common	.	.	.	.	3	.	.	3
P. agricola (Thorell 1856)	6.75	ground hunters	common	.	.	.	.	2	.	1	3
P. cribrata Simon 1876	6.25	ground hunters	common	.	.	.	4	82	61	36	183
P. hortensis (Thorell 1872)	5.25	ground hunters	common	.	.	2	3	13	4	.	22
P. monticola (Clerck 1757)	5.00	ground hunters	common	.	.	.	.	4	.	.	4
P. paludicola (Clerck 1757)	8.50	ground hunters	common	.	.	.	.	4	112	.	116
Pardosa prativaga (L. Koch 1870)	5.00	ground hunters	common	.	.	.	95	303	45	.	443
P. proxima (C.L. Koch 1847)	6.00	ground hunters	common	.	.	.	2	161	164	19	346
P. vittata (Keyserling 1863)	6.30	ground hunters	common	.	.	.	.	48	91	.	139
Pirata latitans (Blackwall1841)	4.50	ground hunters	common	.	.	.	35	63	70	.	168
P. piraticus (Clerck 1757)	6.80	ground hunters	common	.	.	.	.	1	.	.	1
Trebacosa europaea Szinétar & Kancsal 2007	6.25	ground hunters	uncommon	.	.	.	.	7	.	.	7
Trochosa ruricola (De Geer 1778)	11.50	ground hunters	less common	1	.	.	28	94	276	3	402
T. terricola Thorell 1856	11.50	ground hunters	common	.	.	.	.	.	4	.	4
Xerolycosa miniata C.L. Koch 1834	7.00	ground hunters	uncommon	.	.	.	.	1	10	1	12
Mimetidae											
Ero furcata (Villers 1789)	4.00	specialists	common	.	.	.	1	.	.	.	1
Nemesidae											
Brachythele denieri (Simon 1916)	12.50	sensing web	uncommon	17	2	11	4	.	.	.	34
Oonopidae											
Silhouettella loricatula (Roewer 1942)	2.00	ground hunters	uncommon	2	.	.	.	.	.	.	2
Oxyopidae											
Oxyopes heterophthalmus (Latreille 1804)	6.00	other hunters	common	.	.	.	.	.	.	1	1
O. mediterraneus Levy 1999	6.75	other hunters	common	.	2	.	.	.	.	1	3
Philodromidae											
Philodromus pulchellus Lucas 1846	3.85	other hunters	common	.	1	.	.	.	.	.	1
Thanatus atratus Simon 1875	5.30	other hunters	uncommon	38	25	59	33	12	3	36	206
T. striatus C.L. Koch 1845	5.10	other hunters	uncommon	.	.	.	.	.	7	.	7
Tibellus oblongus (Walckenaer 1802)	9.00	other hunters	common	.	.	1	2	.	.	.	3
Pisauridae											
Pisaura mirabilis (Clerck 1757)	13.50	sheet web	common	6	4	3	11	1	3	4	32
Salticidae											
Aelurillus v-insignitus (Clerck 1757)	5.95	other hunters	uncommon	1	5	1	1	.	.	1	9
Ballus chalybeius (Walckenaer 1802)	3.80	other hunters	uncommon	.	1	.	.	.	.	.	1
Chalcoscirtus infimus (Simon 1868)	2.50	other hunters	uncommon	2	5	5	3	.	.	1	16
Euophrys frontalis (Walckenaer 1802)	3.50	other hunters	uncommon	1	.	.	.	.	.	.	1
E. rufibarbis (Simon 1868)	4.25	other hunters	uncommon	1	.	.	.	.	.	.	1
Evarcha arcuata (Clerck 1757)	7.00	other hunters	uncommon	.	.	.	.	.	1	.	1
E. jucunda (Lucas 1846)	6.10	other hunters	uncommon	2	.	.	.	.	.	.	2
Heliophanus auratus C.L. Koch 1835	4.85	other hunters	uncommon	.	.	.	.	1	.	.	1
H. lineiventris Simon 1868	4.95	other hunters	uncommon	.	.	.	.	.	.	1	1
Icius hamatus (C.L. Koch 1846)	5.40	other hunters	common	.	.	1	.	.	.	.	1
Leptorchestes mutilloides (Lucas 1846)	3.70	other hunters	uncommon	1	.	.	.	.	.	.	1
Macaroeris nidicolens (Walckenaer 1802)	5.00	other hunters	common	1	.	.	.	.	.	.	1
Neaetha membrosa (Simon 1868)	4.50	other hunters	uncommon	.	2	.	1	.	.	.	3
Neon rayi (Simon 1875)	2.50	other hunters	uncommon	1	.	.	.	.	.	.	1

APPENDIX—Continued.

Species	Life-history traits			Abundances							
	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Pellenes diagonalis (Simon 1868)	6.50	other hunters	uncommon	.	36	10	.	.	.	.	46
P. nigrociliatus (Simon 1875)	5.30	other hunters	uncommon	.	7	11	.	.	2	3	23
P. seriatus (Thorell 1875)	7.75	other hunters	uncommon	.	.	.	1	.	.	.	1
Philaeus chrysops (Poda 1761)	7.50	other hunters	uncommon	.	1	.	.	.	.	.	1
Phlegra fasciata (Hahn 1826)	6.40	other hunters	common	.	11	6	11	2	3	6	39
P. lineata (C.L. Koch 1846)	3.85	other hunters	less common	.	.	1	.	.	1	.	2
Pseudeuophrys obsoleta (Simon 1868)	4.00	other hunters	less common	6	.	1	.	.	.	.	7
Sitticus penicillatus (Simon 1875)	3.75	other hunters	uncommon	.	.	.	.	.	.	2	2
Synageles dalmaticus (Keyserling 1863)	3.00	other hunters	common	1	.	.	.	.	.	.	1
Talavera aequipes (O.P.-Cambridge 1871)	2.50	other hunters	uncommon	.	.	.	.	.	2	1	3
Scytodidae											
Scytodes thoracica (Latreille 1802)	5.00	other hunters	uncommon	35	4	7	42	1	.	.	89
Sparassidae											
Micrommata virescens (Clerck 1757)	13.50	other hunters	uncommon	.	1	.	.	.	.	.	1
Tetragnathidae											
Pachygnatha clercki Sundevall 1823	5.75	orb web	common	.	.	.	.	1	.	.	1
P. degeeri Sundevall 1830	3.85	orb web	common	.	.	.	2	8	1	.	11
Tetragnatha montana Simon 1874	8.50	orb web	common	.	.	.	1	.	.	.	1
Theridiidae											
Asagena phalerata (Panzer 1801)	4.75	space web	less common	.	2	4	6	1	2	3	18
Crustulina sticta (O.P.-Cambridge 1861)	2.50	space web	less common	.	.	.	.	1	1	.	2
Dipoena coracina (C.L. Koch 1837)	2.00	space web	common	.	.	2	.	1	5	.	8
Enophlognatha thoracica (Hahn 1833)	3.75	space web	common	1	.	.	1	1	.	1	4
Episinus truncatus Latreille 1809	5.00	space web	uncommon	1	.	.	.	.	.	.	1
Euryopis episinoides (Walckenaer 1847)	3.00	space web	common	.	.	1	.	.	.	.	1
E. quinqueguttata Thorell 1875	2.50	space web	common	2	.	1	1	.	.	1	5
Latrodectus tredecimguttatus (Rossi 1790)	13.00	space web	less common	.	.	.	.	.	.	1	1
Pholcomma gibbum (Westring 1851)	1.70	space web	uncommon	2	.	.	.	.	.	.	2
Robertus mediterraneus Eskov 1987	3.50	space web	less common	.	.	.	.	.	1	.	1
Steatoda albomaculata (De Geer 1778)	6.00	space web	less common	.	4	.	.	.	.	.	4
Theridion cinereum Thorell 1875	3.20	space web	common	.	.	.	1	.	.	1	2
Thomisidae											
Monaeses israeliensis Levy 1973	8.50	ambush hunters	uncommon	.	.	.	1	.	.	.	1
Ozyptila cf. *sanctuaria*	3.50	ambush hunters	common	.	9	12	4	.	.	6	31
O. praticola (C.L. Koch 1837)	3.50	ambush hunters	common	.	.	.	3	.	.	.	3
O. simplex (O.P.-Cambridge 1862)	4.50	ambush hunters	common	.	.	.	.	1	.	.	1
Runcinia grammica (C.L. Koch 1837)	6.35	ambush hunters	uncommon	.	.	.	.	.	.	2	2
Synema plorator (O.P.-Cambridge 1872)	5.90	ambush hunters	less common	.	2	7	.	.	.	.	9
Xysticus caperatus Simon 1875	7.30	ambush hunters	common	9	4	37	34	1	1	24	110
X. cristatus (Clerck 1757)	6.35	ambush hunters	common	.	1	1	1	.	1	.	4
X. gallicus Simon 1875	9.00	ambush hunters	common	.	2	2	.	.	1	1	6
X. graecus C.L. Koch 1837	8.45	ambush hunters	common	.	.	1	.	.	.	.	1
X. kempelini Thorell 1872	6.55	ambush hunters	common	2	2	.	10	.	1	.	15
X. kochi Thorell 1872	8.45	ambush hunters	common	2	40	32	7	4	14	10	109
X. luctator L. Koch 1870	8.50	ambush hunters	common	.	.	.	1	.	.	.	1
X. robustus (Hahn 1832)	9.50	ambush hunters	common	.	4	3	.	.	.	1	8
X. xerodermus Strand 1913	7.75	ambush hunters	common	.	2	.	.	.	2	.	4
Titanoecidae											
Nurscia albomaculata (Lucas 1846)	10.50	space web	uncommon	.	2	2	5	8	8	2	27
Titanoeca flavicoma L. Koch 1872	6.10	space web	uncommon	.	48	84	5	11	4	26	178
T. turkmenia Wunderlich 1995	4.80	space web	uncommon	.	.	.	.	.	.	7	7
Zodaridae											
Zodarion epirense Brignoli 1984	4.25	specialists	uncommon	.	.	1	2	.	.	2	5
Z. frenatum Simon 1884	4.00	specialists	uncommon	2	11	12	9	.	2	10	46
Z. granulatum Kulczyn'ski 1908	2.30	specialists	uncommon	.	.	.	1	.	.	.	1
Z. morosum Denis 1935	5.55	specialists	uncommon	.	9	9	3	.	1	4	26
Z. thoni Nosek 1905	4.10	specialists	uncommon	.	2	.	.	.	.	.	2
Zoridae											
Zora armillata Simon 1878	5.25	ground hunters	common	.	.	.	1	1	.	.	2
Z. parallela Simon 1878	4.95	ground hunters	common	.	.	1	.	.	.	.	1
Z. silvestris Kulczyn'ski 1897	3.75	ground hunters	common	.	.	.	.	1	.	.	1