

Seasonal activity of the ground spider fauna in a Mediterranean ecosystem (Mt Youchtas, Crete, Greece)

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Summary

Arachnological data on the ground faunas of the eastern Mediterranean island ecosystems are very scarce, usually concerned with descriptions of new taxa or reviews of distributional data of the known species of the area. An ecological approach is limited and almost absent at post-family level. The scope of the present work is the structure of the spider community (family and species composition) as well as spider kinetic activity during the period of one year, in a Mediterranean phryganic ecosystem (north-east slopes of Mt Youchtas, 16 km south of the city of Irakleion, Crete). Spiders were sampled monthly, using 25 pitfall traps placed under the dominant plant species of the site (Broom, Thyme and Kermes Oak) and on the open ground. A total of 1845 individuals were captured throughout the year, belonging to 21 families and 61 species. The dominant families as far as both species richness and abundance are concerned were Gnaphosidae, Linyphiidae and Salticidae, with the rest of the families much less well represented. Seasonal variation revealed three basic patterns of activity, indicating differences in life style and responses to environmental factors. Spatial variation was limited only by minor differences between open ground areas and those covered by the dominant plants of the site.

Introduction

Spiders are generalist feeders with great species richness in every type of terrestrial habitat, and therefore they play an important role in the structure of communities and food webs, both as number of individuals and as energy consumers (Post & Riechert, 1977; Foelix, 1982; Fasola & Mogavero, 1995). These features make them ideal models as terrestrial predators in community analyses (Post & Riechert, 1977; Wise, 1993). Ecological studies of this kind have been presented in the past, mainly concerning the relationships between taxonomically well-defined groups of spider species in regions in which problems on spider taxonomy are more or less resolved. Knowledge of species composition and distribution in eastern Mediterranean ecosystems is very limited, making ecological studies in this region very difficult.

Arachnological data on the ground faunas of ecosystems in Greece have been provided by researchers such as Brullé (1832), Lucas (1853), Kulczyński (1903), Strand (1916), Roewer (1928, 1959) and Bristowe (1934), who presented lists of the spider species of several continental and insular sites of Greece with some ecological notes. A more detailed study of the region was carried out later by Brignoli, who produced many papers on spider taxonomy with biogeographical notes, in the period 1968–1986 (Brignoli, 1984, and references therein, 1985, 1986). He concentrated mainly on cave spiders. Contemporary researchers are making further contributions with descriptions of new species and/or distributional data on the spider fauna of the same area.

Species catalogues on a national or regional level are still unavailable for Greece, while the contribution of Greek scientists has been limited (Chatzisarantos, 1940; Paraschi, 1988).

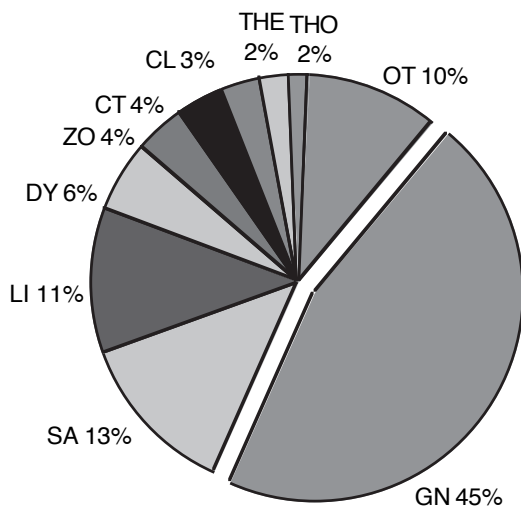


Fig. 1: Dominant spider families on an annual scale. GN = Gnaphosidae, SA = Salticidae, LI = Linyphiidae, DY = Dysderidae, ZO = Zodariidae, CT = Ctenizidae, CL = Clubionidae, THE = Theridiidae, THO = Thomisidae, OT = Others.

Neither the main characteristics nor the individual details of the Greek arachnofauna are well known. Apart from the ecological data on Greek spiders of the maquis of the central Aegean provided by Paraschi (1988), no other data are available on the arachnofaunas of the southern Greek ecosystems.

The present work focuses on the basic structure of spider communities (family and species composition, dominant taxa), on the family and dominant species phenologies, as well as on the life strategies of the arachnofauna, in the south Aegean phrygic ecosystems. An effort has also been made to reveal spatial differentiation in different microbiotopes of the study area.

Materials and methods

The study area is situated on the north-eastern slopes of Mt Yuchtas (highest point 811 m), 16 km south of the city of Irakleion, north-central Crete, and is about 350 m above sea level. The substrate is calcareous with many stones and rocks, while the slope of the site varies between 20–40%. The vegetation can be described as degraded maquis and phrygana,

including dwarf, aromatic and thorny shrub species characteristic of the Cretan landscape such as: *Genista acanthoclada*, *Coridothymus capitatus*, *Ebenus creticus*, *Salvia fruticosa*, *Asphodelus aestivus*, *Cistus creticus*, as well as taller shrubs of *Quercus coccifera*. Plants cover about 80% of the site; the remaining 20% is open ground. The area chosen for this study, although quite close to urban, pastoral and agricultural regions, is undisturbed by human activities (grazing of animals is prohibited), and has been proposed for inclusion in the NATURA 2000 EEC network of protected areas (on account of high levels of biodiversity and plant endemism). It is quite close to the University, facilitating monthly visits.

Twenty-five pitfall traps were placed under the dominant plant species (*Quercus coccifera*, *Genista acanthoclada*, *Coridothymus capitatus*, *Ebenus creticus*, *Salvia fruticosa*) and on the open ground. The traps were plastic cans (12 cm high, 9.5 cm diameter); the killing agent and preservative fluid used was ethylene glycol. Spiders and other arthropods were sampled monthly and the samples were sorted and stored in 70% alcohol. The sampling period lasted from December 1995 to January 1997. The results of the first twelve months are presented here, while data of the remaining two months have been used as a control.

Spiders were sorted, identified, counted and deposited in the Natural History Museum of the University of Crete. Some of the identifications as well as species confirmations were carried out by Dr K. Thaler, Institut für Zoologie, Innsbruck. Immature specimens were identified to below family level when possible.

In order to equalize the number of individuals for each month, all monthly catches were transformed into number of individuals per 30 trap days.

Principal Component Analysis (PCA) and Correspondence Analysis (CA) were used for the spatial differentiation analysis for each month (Pielou, 1984).

Results

Faunal composition and abundances

A total of 1845 individuals were captured during the one-year sampling, belonging to 21

families and 61 species. Gnaphosidae can be classified as the dominant family (over 40% annual representation), while the rest of the families belong to influent (16–23%) or accessories (below 8%), following the classification of Łuczak (1963) (Fig. 1).

Family composition of the spider community shows considerable variability from month to month. Gnaphosidae represent the dominant family for most of the months, ranging from 2% (December) to 77% (May). Linyphiidae dominate during the winter and spring months, ranging from 2% (May) to 63% (December), but are absent during the summer and autumn. Salticidae reach their maximum abundance in September (34%). The rest of the families represent less than 10% of the total arachnofauna, with their maximum monthly abundance being less than 25%.

The three dominant families, Gnaphosidae, Linyphiidae and Salticidae, are also the most numerous as far as species richness is concerned: Linyphiidae are represented by 10 species, Gnaphosidae by 10 species, Salticidae by 9 species. Some families are represented by 4 or 5 species (such as Dysderidae, Theridiidae and Thomisidae), while the majority of the families are represented by only one or two species.

The commonest taxa collected at the site were *Pterotricha lentiginosa* (Koch, 1839), *Walckenaeria cretaensis* (Wunderlich, 1994), *Drassodes*, *Zelotes*, *Lepthyphantes*, *Dysdera*, *Harpactea*, *Cyrtocarenum* and *Crustulina* (Table 1).

It is interesting to note that, although the highest numbers of spiders were collected in spring and autumn, the greatest numbers of species were reported in summer. During July there is a maximum of families (17) represented in the site, while the minimum is in December (7). This coincides with observations of other researchers on grasslands (Duffey, 1962), but in other cases this summer maximum in species richness is mirrored by similar peaks in absolute numbers (Merrett & Snazell, 1983).

Phenology—temporal variation

The annual spider activity in the study area is illustrated in Figure 2. Two peaks of activity occur, one in spring (from April to June) and one (slightly higher) in autumn (September). Monthly fluctuations in activity are mainly

Agelenidae *Maimuna* cf. *cretica*, *Tegenaria* sp.; **Amaurobiidae** *Amaurobius* cf. *erberi*; **Anyphaenidae** *Anyphaena sabina*; **Clubionidae** *Clubiona vegeta*?, *Mesiotelus* cf. *tenuissimus*; **Ctenizidae** *Cyrtocarenum cucicularium*; **Dysderidae** *Dysdera gigas*, *Harpactea coccifera*, *H. cressa*, n. sp.; **Filistatidae** *Filistata* (*Pritha*) sp., *Filistata insidiatrix*; **Gnaphosidae** *Aphantaulax seminigra*, *Drassodes lapidosus*, *D. lutescens*, *Haplodrassus dalmatensis*? *H. signifer*, *Nomisia* cf. *ripariensis*, *Pterotricha lentiginosa*, *Zelotes* (*Drassyllus*) sp., *Zelotes* cf. *creticus*, *Zelotes* sp.; **Linyphiidae** *Gonatium* sp., *Lepthyphantes* aff. *collinus*, *Mecopisthes* sp., n. sp., *Pelecopsis* sp., *Savignya*? sp., *Sintula retroversus*, *Theonina* sp., *Walckenaeria clavilobus*, *W. cretaensis*; **Loxoscelidae**? (immature specimen); **Lycosidae** *Lycosa narbonensis*; **Oecobiidae** *Oecobius* sp.; **Oonopidae** *Oonops* sp.; **Oxyopidae** *Oxyopes heterophthalmus*; **Palpimanidae** *Palpimanus* sp.; **Pholcidae**? (immature specimen); **Salticidae** *Aelurillus* sp., cf. *Aelurillus*, *Ballus* sp., *Cyrra algerina*, *Euophrys* sp., *Heliophanus* sp., *Pellenes*?, *Philaeus chrysops*, *Saitis graeca*?; **Scytodidae** *Scytodes thoracica*; **Theridiidae** *Crustulina scabripes*, *Enoplognatha thoracica*, *Episinus* sp., *Euryopis sexalbomaculata*, *Theridion* cf. *melanurum*; **Thomisidae** *Ozyptila confluens*, *Proxysticus* sp., *Thanatus vulgaris*, *Xysticus turcicus*; **Zodariidae** *Zodarion* sp. 1, *Zodarion* sp. 2.

Table 1: List of species in the study area.

influenced by the activity of males. When mature, males become very active in the effort to find a mate. Therefore, the great number in pit-fall catches is indicative of the time of reproduction (Tretzel, 1954; Duffey, 1962; Milner, 1988). The spring peak is produced both by male and female individuals, though the autumn peak is formed mainly by the male activity. Immatures are more abundant during spring and late summer, indicating that the reproductive period of most of the spiders is in the spring.

When referring to the seasonal activity on a family level, three basic patterns are apparent, formed by the three dominant families, Gnaphosidae, Linyphiidae and Salticidae (Fig. 3). These patterns of activity fit to Eurychronous, Winter-mature and Stenochronous modes, respectively, as defined by Aitchison (1984).

Eurychronous families. Gnaphosidae are present during the whole year, with two peaks of activity in May (males and females) and September (almost only males), while during the

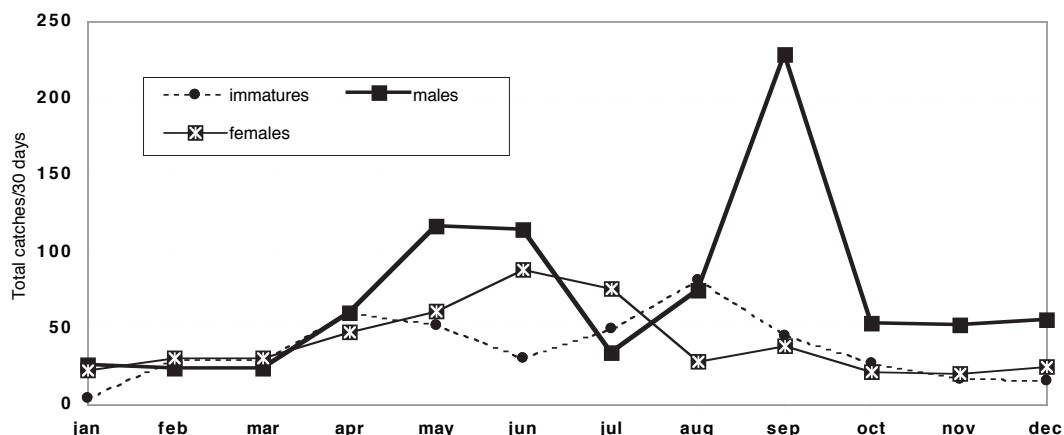


Fig. 2: Spider phenology on Mt Youchtas.

winter they are almost exclusively represented by immature individuals and some females of the genus *Zelotes*. *Pterotricha lentiginosa* and *Zelotes* spp. are the most abundant species, forming the main pattern of activity of the family, while *Nomisia* and *Drassodes* spp. are less well represented in this pattern, being active mostly during April and May (therefore showing a more stenochronous mode of activity, see Fig. 4). Members of the families Zodariidae, Palpimanidae and Thomisidae can also be included in this category.

Winter-active families. Linyphiidae constitute the majority of the arachnofauna in winter (occupying 63% of the total catch in December), while they decline during the dry season (from May to October). *Walckenaeria* and *Lepthyphantes* spp. seem to have a longer period of activity than other species. In higher latitudes, some Linyphiidae present another peak in autumn (Huhta, 1971); this does not occur in the study area because the temperatures in Crete are still quite high during the same period, which does not encourage a second generation of linyphiids.

Clubionidae and Dysderidae are apparently winter-active spiders, showing a pattern of activity very similar to that of Linyphiidae. All three together constitute almost the total spider catch in winter and early spring.

The main peak of activity in Dysderidae is produced by all dysderid species found at the site. However, the second peak in November is

formed by the presence of male individuals only of *Dysdera gigas* Roewer, 1928. The same pattern is shown by Clubionidae, where the November peak is produced mainly by the males of the *Mesiotelus* spp.

Amaurobiidae seem to follow the same pattern, but no safe conclusion can be drawn because of the low numbers of specimens collected.

Stenochronous families. Salticidae seem to have a reverse pattern of activity, showing a maximum peak in September (formed mostly by males) and a lower one in June (males and females), representing a more xerophilous behaviour. Salticidae (greatly diversified in Crete) is represented by a good number of species in the study area; when present, they are active almost all the time,

Ctenizidae, Theridiidae, Filistatidae, Oecobiidae, Loxoscelidae, Pholcidae, Scytodidae and Lycosidae follow the stenochronous pattern of Salticidae, being active for only one period of the year, with the immature phase preceding or following. A continuous series of activity peaks from late summer to early autumn precludes any strict categorization of the above families into seasonal types. Ctenizidae and Lycosidae were mostly represented by males, which is to be expected considering the mode of life of these families—females of *Cyrtocarenum cunicularium* Olivier, 1811 and *Lycosa narbonensis* (Latreille, 1806) do not leave their burrows for most of their lives. Most of the Scytodidae collected in the traps were

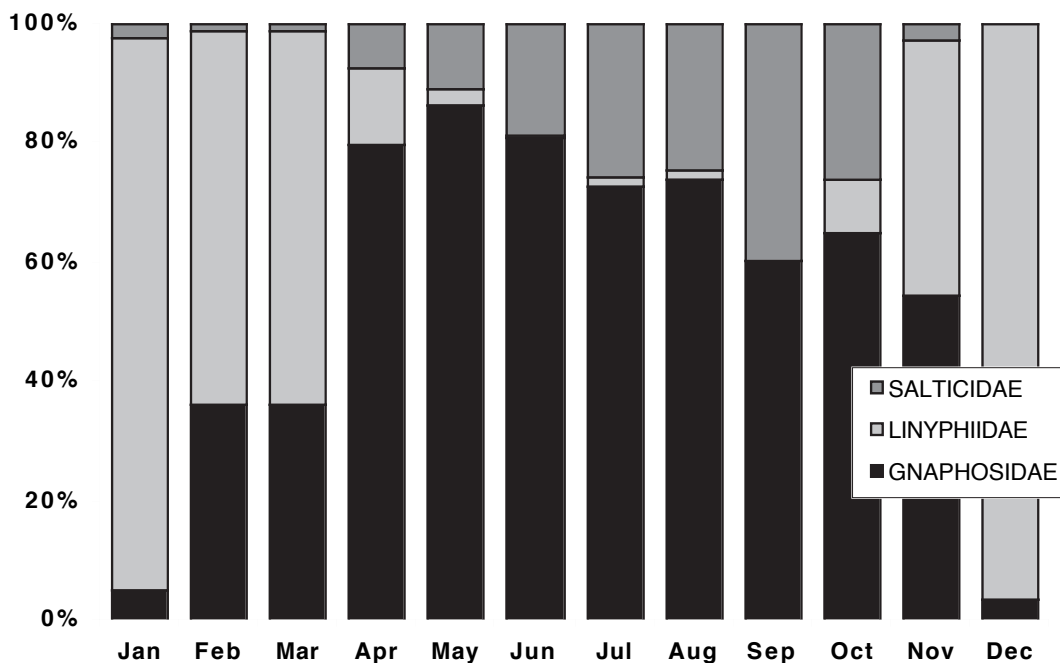


Fig. 3: Relative representation of numbers of individuals of the families Salticidae, Linyphiidae and Gnaphosidae.

immatures, suggesting a non-errant mode of life of adults. Oecobiidae are active almost exclusively in June, with a high representation of both males and females.

Theridiidae spend their lives almost exclusively on the lower vegetation, so their densities may be much higher than those indicated by pit-fall trapping. Little can be said about Filistatidae, Loxoscelidae and Pholcidae, due to the low number of specimens collected.

In an overall view, stenochronous and eurychronous families constitute the spider community of the dry season, which in Crete lasts from May until October. If any specific strategies are included in these patterns of activity, they seem to adapt their agents in the best way for their survival in the dry habitats of the eastern Mediterranean.

Spatial variation

As mentioned before, the 25 pitfall traps were placed under the dominant plant species and on the open ground, in order to reveal differences in the spatial distribution of spiders in the microhabitats of the site. Principal Component

Analysis (PCA) was used to detect significant differences among the 25 traps, depending on the composition of the families found in them. Numbers of individuals in each trap were square root-transformed and the analysis was performed for each month separately. When the first PCs were plotted there was no evident grouping of the traps relating to microhabitats and the composition of families found in them.

The 25 traps were then divided into the corresponding microhabitats and manipulated as six different substations to be analysed with Correspondence Analysis (CA). The analysis could not provide clues about any preference of a particular family to a specific microhabitat when viewed on an annual scale, except that *Quercus*, *Thymus*, and open ground produced the highest numbers of spiders. On the other hand, the following results can be extracted from the monthly analyses:

- Collections from the six substations were quite distinct each month.
- Linyphiidae showed some preference for the *Ebenus* microhabitat (December to March),

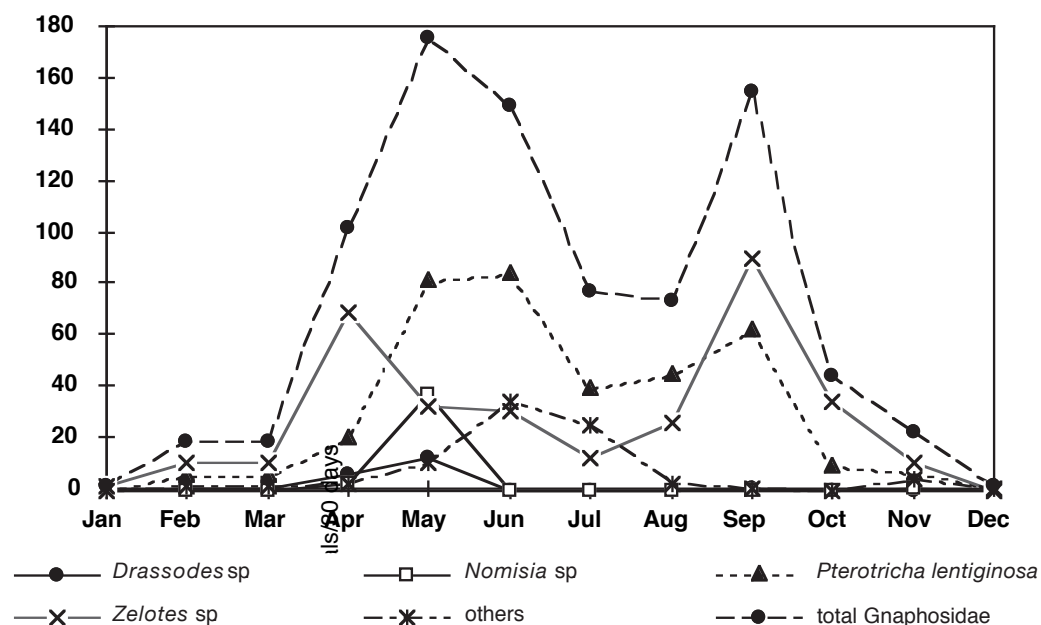


Fig.4: Phenology of the dominant Gnaphosidae on Mt Youchtas.

though in November they seemed to prefer the open ground.

- Gnaphosidae and Salticidae did not show a special preference for any microbiotope, being abundant everywhere and moving constantly.

- Ctenizidae showed a drift from the open ground (June and July) to microbiotopes covered by vegetation (August to December).

- Theridiidae and Thomisidae showed a clear avoidance of the open ground. The former were found more often in the *Quercus* and *Genista* microbiotopes, while the latter did not show any evident preference.

- Dysderidae showed a preference for the *Quercus* microbiotope, while during July and August (when only immature individuals occur in the site) they were also present on the open ground.

- Filistatidae tended to be present more frequently on the open ground through the whole year.

- Agelenidae showed some preference for *Genista* and *Salvia*.

- Oecobiidae occurred more frequently on the open ground.

Discussion

Although pitfall trapping selectively collects only the ground active spiders (Duffey, 1962; Southwood, 1966; Turnbull, 1973), it is, nevertheless, a suitable method for semi-quantitative analyses—the measurement of “active density” (Uetz & Unziker, 1976), or “penetration” (Heydemann, 1961)—and can give a comparative measure of communities without the bias of the different collecting abilities of researchers.

The total number of catches (1845 individuals with mean density of 30.7 individuals per station per month), as well as the number of families (21) and species (59) found in the study area, are similar to those reported by other authors in Mediterranean ecosystems: 26 families in a phrygane ecosystem in Lebanon (Assi, 1983); 15–17 families in arid grasslands and *Juniperus* associations in New Mexico (Muma, 1980); 22 families in a *Quercus coccifera* association in southern France (Bigot & Bodot, 1972); and 20–22 families in the maquis ecosystem of Epidaurus and Naxos in Greece (Paraschi, 1988). These numbers, when compared with similar studies from other types of ecosystems in central Europe, suggest that the heterogeneity of

Mediterranean ecosystems, especially the insular ones, produces higher diversities, but lower population densities (Di Castri & Vitali-Di Castri, 1981).

In overall view, wandering, ground-living spiders dominate the site, constituting about 71% of the total arachnofauna of the year, which is to be expected for insular, east Mediterranean, phrygic ecosystems (Bristowe, 1929; Herzog, 1961; Moyano *et al.*, 1986). On the other hand, Linyphiidae, a characteristic family of cold and temperate climates, is the third commonest family in the study area, being active only during the colder and moister season, i.e. in winter. Linyphiids also show high diversity in many regions of southern Greece (Paraschi, 1988).

Gnaphosidae is the predominant family as far as both species richness and population densities are concerned. Mediterranean (*Pterotricha lentiginosa*), east Mediterranean (*Nomisia* sp.), or south European (*Zelotes* spp., *Drassodes* spp.) species were the most abundant gnaphosids in the study area. The dominance of Gnaphosidae is to be expected in dry habitats as they are equally represented in maquis or phrygana of insular and continental Greece (Paraschi, 1988).

Salticidae is represented by a good number of species (9) and great population densities when compared with most of the other families at the site. However, our data underestimate the contribution of Salticidae in the study area, when compared with the 23 species found in the maquis of the central Aegean (Paraschi, 1988). This is probably because pitfall trapping alone is not an efficient method of sampling salticids (Merrett & Snazell, 1983). The data on the central Aegean spiders (Paraschi, 1988) were produced by pitfall trapping, quadrats, hand collecting, and other methods.

The presence of Ctenizidae is characteristic of east Mediterranean habitats; Dysderidae also diversify greatly in many Greek regions, with many endemic representatives, while Zodariidae are represented here by two species possibly new to science. Theridiidae are much less well represented on Mt Youchtas than in similar ecosystems, where they can be considered as dominant (Paraschi, 1988). This may be because pitfall traps collect only members that live in the litter, and not species from the vegetation above (Merrett & Snazell, 1983).

The spider phenology of the study area coincides with these of other arthropods in Mediterranean ecosystems (Di Castri & Vitali-Di Castri, 1981; Lamotte & Blandin, 1989; Magioris, 1991), presenting two peaks of activity, one in spring and one in autumn. The adaptations of spiders to the bioclimatic seasonality (being influenced basically by the day length and/or temperature) are evident here, reflecting the intensity of trophic interchanges of Mediterranean ecosystems during the period from spring to autumn (Pearson & White, 1964; Iatrou & Stamou, 1989; Lamotte & Blandin, 1989).

A closer analysis of the patterns of different families proves that the second peak in September is mainly produced by male members of the families Gnaphosidae and Salticidae, thus the best adapted families into the area, whereas winter-active families form a totally different pattern of activity, dominating the area only in the moist season.

The two-peak activity pattern, when present, indicates a diplochronous type of development. It may be explained either by the existence of two generations per year (Juberthie, 1954), or by only one year-long adult period (assuming that the pitfall traps are unable to record the full extent of the adult period, as the species are caught during their activity periods only) as proposed by Toft (1976). As stated by the same author, copulation may take place in the autumn (as indicated by the large peak of males in September), whereas egg development is postponed until late spring and summer, as indicated by the peak of females in May–June–July, followed by a peak of immatures just afterwards (August). The smaller peak of males in spring is produced by males surviving the winter period. This interpretation also accords with the opinion of Tretzel (1954), that maxima of males indicate the period of copulation, whereas those of female activity are connected with food-capturing during the period of egg-development. However, if life cycles of species are not well known, no definite conclusions can be drawn from the interpretation of pitfall data.

Finally, when possible groupings of the different microhabitats based on the composition of spider families were checked, only slight preferences of some families towards a microhabitat could be detected, even though the six

microbiotopes were quite distinct. As stated by Merrett & Snazell (1983), this may be because pitfall trapping is unable to reflect differences among the higher strata of vegetation, thus producing a less clear grouping of sites.

Acknowledgements

We are very grateful to Dr K. Thaler for his help in the systematic part of this study. We also wish to thank Mr S. Chatzimanolis for the sorting and counting of the rest of the arthropods trapped.

References

- AITCHISON, C. W. 1984: The phenology of winter-active spiders. *J. Arachnol.* **12**: 249–271.
- ASSI, F. 1983: *Recherches écologiques sur le peuplement des araignées d'une garrigue du Liban*. Thèse Dr d'État, Université de Paris IV.
- BIGOT, L. & BODOT, P. 1972: Contribution à l'étude biocoenotique de la garrigue à *Quercus coccifera*. I. Étude descriptive de l'habitat et de la faune des invertébrés inventoriés. *Vie Milieu* **23**: 23–43.
- BRIGNOLI, P. M. 1981: Vue d'ensemble sur les araignées de Grèce (Araneae). *Biologia gallo-hellen.* **10**: 161–169.
- BRISTOWE, W. S. 1929: The distribution and dispersal of spiders. *Proc. zool. Soc. Lond.* **1929**: 633–657.
- BRISTOWE, W. S. 1934: The spiders of Greece and the adjacent islands. *Proc. zool. Soc. Lond.* **1934**: 733–788.
- BRULLÉ, A. 1832: *Expédition scientifique de Morée. Tome III, 1e Partie: Zoologie; 2e Section: Des animaux articulés*. Paris.
- CHATZISARANTOS, C. 1940: *Spiders of Attiki*. Ph.D. thesis, University of Athens.
- DI CASTRI, F. & VITALI-DI CASTRI, V. 1981: Soil fauna of Mediterranean-climate regions. In *Ecosystems of the world*, **11**. Amsterdam, Oxford, New York: Elsevier: 445–478.
- DUFFEY, E. 1962: A population study of spiders in limestone grassland. *J. anim. Ecol.* **31**: 571–599.
- FASOLA, M. & MOGAVERO, F. 1995: Structure and habitat use in a web-building spider community in northern Italy. *Boll. Zool.* **62**: 159–166.
- FOELIX, R. F. 1982: *Biology of spiders*. 1st ed. Cambridge, MA & London: Harvard University Press.
- HERZOG, G. 1961: Zur Ökologie der terrestren Spinnenfauna märkischen Kiefernheiden. *Ent. Z., Frankf. a. M.* **71**: 1–11.
- HEYDEMANN, B. 1961: Untersuchungen über die Aktivitäts- und Besiedlungsdichte bei epigäischen Spinnen. *Verh. dt. zool. Ges.* **35**: 538–556.
- HUHTA, V. 1971: Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. *Annls zool. fenn.* **8**: 483–542.
- IATROU, G. D. & STAMOU, G. P. 1989: Preliminary studies on certain macroarthropod groups of a *Quercus coccifera* formation (Mediterranean-type ecosystem) with special reference to the diplopod *Glomeris balcanica*. *Pedobiologia* **33**: 301–306.
- JUBERTHIE, C. 1954: Sur les cycles biologiques des araignées. *Bull. Soc. Hist. nat. Toulouse* **89**: 299–318.
- KULCZYŃSKI, W. 1903: Collected papers on spiders of Władysław Kulczyński. *Bull. Acad. Sci. Cracovie* **26**: 32–58.
- LAMOTTE, M. & BLANDIN, P. 1989: Originalité et diversité des écosystèmes méditerranéens terrestres. *Biologia gallo-hellen.* **16**: 5–36.
- LUCAS, M. H. 1853: Essai sur les animaux articulés qui habitent l'île de Crète. *Revue Mag. Zool.* **5**: 514–531.
- LUCZAK, J. 1963: Differences in the structure of communities of web spiders in one type of environment (young pine forest). *Ekol. pol.* **11**: 159–221.
- MAGIORIS, S. 1991: *Ecology of ground arthropods of insular phrygane ecosystems and of a degraded maquis ecosystem*. Ph.D. thesis, University of Athens.
- MERRETT, P. & SNAZELL, R. 1983: A comparison of pitfall trapping and vacuum sampling for assessing spider faunas on heathland at Ashdown Forest, south-east England. *Bull. Br. arachnol. Soc.* **6**: 1–13.
- MILNER, J. E. 1988: Oxleas Wood: Observations on the spiders, their phenology and ecological strategies. *Lond. Nat.* **67**: 97–118.
- MOYANO, F. J., PASCUAL, F. & JIMÉNEZ, E. 1986: Characterization of a spider community. I. Temporary and spatial distribution. In J. A. Barrientos (ed.). *Actas X Congreso Internacional de Aracnología Jaca (España)*, **I**. Barcelona: Instituto Pirenaico de Ecología (C.S.I.C.) and Grupo de Aracnología (Assoc. esp. Entomol.): 276.
- MUMA, M. H. 1980: Comparison of ground-surface spider populations in Pinyon-Juniper and arid-grassland associations in southwestern New Mexico. *Fla Ent.* **63**: 211–221.
- PARASCHI, L. 1988: *Study of spiders in maquis ecosystems of southern Greece*. Ph.D. thesis, University of Athens.
- PEARSON, R. G. & WHITE, E. 1964: Factors contributing to the annual cycles of surface-active arthropods in moorland country. *Entomologist's mon. Mag.* **100**: 201–206.

- PIELOU, E. C. 1984: *The interpretation of ecological data*. New York: Wiley.
- POST, W. M. & RIECHERT, S. E. 1977: Initial investigation into the structure of spider communities. *J. anim. Ecol.* **46**: 729–749.
- ROEWER, C. F. 1928: XI. Araneae. In *Zoologische Streifzuege in Attika, Morea und besonders auf der Insel Kreta*. *Abh. naturw. Ver. Bremen* **27**: 92–123.
- ROEWER, C. F. 1959: Die Araneae, Solifuga und Opiliones der Sammlungen des Herrn Dr. K. Lindberg aus Griechenland, Creta, Anatolien, Iran und Indien. *Göteborgs K. Vetensk.-o. vitterhSamh. Handl.* **8**: 3–47.
- SOKAL, R. R. 1979: Testing statistical significance of geographic variation patterns. *Syst. Zool.* **28**: 227–232.
- SOUTHWOOD, T. R. E. 1966: *Ecological methods with particular reference to the study of insect populations*. London: Methuen & Co.
- STRAND, E. 1916: Arachnologica varia XX. Spinnen und Opilionen aus Griechenland, Albanien und Kleinasien. *Arch. Naturg.* **82A**: 158–167.
- TOFT, S. 1976: Life-histories of spiders in a Danish beech wood. *Natura Junl.* **19**: 5–40.
- TRETZEL, E. 1954: Reife und Fortpflanzungszeit bei Spinnen. *Z. Morph. Ökol. Tiere* **42**: 634–691.
- TURNBULL, A. L. 1973: Ecology of the true spiders (Araneomorphae). *A. Rev. Ent.* **18**: 305–348.
- UETZ, G. W. & UNZICKER, J. D. 1976: Pitfall trapping in ecological studies of wandering spiders. *J. Arachnol.* **3**: 101–111.
- WISE, D. H. 1993: *Spiders in ecological webs*. Cambridge: Cambridge University Press.