

ECOLOGICAL PROFILES OF HARVESTMEN (ARACHNIDA, OPILIONES) FROM VITOSHA MOUNTAIN (BULGARIA): A MIXED MODELLING APPROACH USING GAMS

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ABSTRACT. The present study is based on a large-scale sampling program carried out in the area of Vitosha Mountain (Bulgaria). The ecological profiles of the Opiliones inhabiting the investigated area are modelled by a mixed approach, using Generalized Additive Models (GAMs) over a Multiple Correspondence Analysis (MCA, performed on the sites by environmental variables matrix) ordination plot. According to the literature data describing the harvestmen species from Vitosha Mountain, the most important factor determining the ecological classification of the Opiliones is the habitat type. The modelled ecological profiles revealed that the elevation contributes the most to the ecological characterization of the Vitosha harvestmen species, followed by the habitat type and moisture regime of the sampling localities. Few harvestmen species demonstrate preferences to the middle- and high-mountain zones, while the majority of harvestmen species are confined exclusively to the low-mountain zone. The different species showed different responses (most of them were linear, not unimodal) towards the environmental variables.

Keywords: Ecological type, ecological classification, Opiliones, Bulgaria, Generalized Additive Models, Multiple Correspondence Analysis

Traditionally, studies on Opiliones in Bulgaria have been predominantly faunistic and taxonomic (Staręga 1976; Martens 1978; Beron & Mitov 1996; Mitov 1987, 1994, 1995a, 1997a, 2001, 2002, 2003, 2004; Mitov & Stoyanov 2004), while data about the biology and ecology of the group are comparatively scarce and scattered through the faunistic literature (Staręga 1976; Martens 1978; Mitov 1986, 1995b,c, 1996, 1997b, 2000, in press; Mitov & Stoyanov 2004). Even on a European scale the ecological research on this animal group remains insufficient. However, the works of Todd (1949), Pabst (1953), Pfeifer (1956), Williams (1962), Kolosváry (1966b), Tischler (1967), Weiss (1975, 1978, 1984, 1996), Obrtel (1976), Curtis (1978), Weiss & Sârbu (1977), Hiebsch (1978), Bliss & Tietze (1984), Klimeš & Špičáková (1984), Klimeš (1987, 1990, 2002), Sechterová (1989), Platen (1991, 1996, 2000), Simon (1995), Novak et al. (2004), Komposch & Gruber (1999), Lymberakis et al. (in press) are specially dedicated

to various aspects of the harvestmen ecology. Additional ecological notes may be found in the mostly faunistic studies of Cîrdei & Bulimar (1960), Hiebsch (1972), Meijer (1972), Thaler (1979), Müller (1984), Komposch (1995, 1997a,b,c, 1999, 2000, 2001, 2004), Platen et al. (1991), Platen & Broen (2002), Metzén & Cölln (1998), Komposch & Gruber (2004), in annotated species lists.

Many of these publications contain ecological classifications of harvestmen species, based on their affinities towards certain environmental conditions. These classifications are often based on the subjective evaluation of the author. For example, *Lophopilio palpinalis* (Herbst 1799) has been described as “stenotopic?” (Komposch 1997a) on one hand, and as “moderately eurytopic” and “vertical-ubiquistic” (Kolosváry 1965; Komposch 1999) on the other. Further, investigators go into even more detail by classifying this species also as “hemiombrophilous/ombrophilous” (Pfeifer 1956; Weiss 1975; Bliss & Tietze

1984; Mitov & Stoyanov 2004), “psychrophilous” (Mitov & Stoyanov 2004), “hemihygrophilous/hygrophilous forest form” (Weiss 1975; Martens 1978; Geyer 1983; Bliss & Tietze 1984; Müller 1984; Platen et al. 1991, 1996, 2000; Komposch 1997a,b, 1999; Metzzen & Cölln 1998; Platen & Broen 2002). These categorizations may have a significant empirical background, but often the ecological type of a species is confusing without detailed reference to the analytical procedures that led to them. So the above mentioned discrepancies might be a manifestation of Kühnelt’s principle of regional stenocoecy (e. g. Kühnelt 1965) or due to subjective error. Recently, with the development of more elaborate modelling techniques that permit a direct relation between the species and their environment, attempts have been made to directly explore the responses of harvestmen species to various environmental variables by employing multivariate techniques (Klimeš 1997; Muster 2001). Subjecting a significant amount of data from the Czech Republic to multivariate analytical procedures (such as TWINSPAN and CCA), Klimeš (1997) concluded that the main factors explaining the variation of the data were elevation, temperature and human impact. Muster (2001) found that the harvestmen from the central part of N Alps were also mostly affected by elevation and light conditions. Both these works employed Canonical Correspondence Analysis (CCA; ter Braak 1987), a widely used method for direct (“constrained”) gradient analysis, that assumes species to have unimodal distributions along environmental gradients, but none of them tested if this crucial assumption of CCA was met by the data. Consequently, the interpretations may be influenced by potential non-unimodal species responses. Nevertheless, these works may be regarded as first attempts to put the relationships between harvestmen and their habitat on an objective basis. In view of these considerations, the present work will aim at contributing further to the knowledge of autecological features of the opilionid species from the Vitosha Mountains (the region in Bulgaria with the most fully studied opilionid assemblages; see Mitov 2000) by direct modelling the response of each species towards an array of environmental factors.

Utilizing an extensive data set from a large-scale sampling program, we will focus on: 1)

summarizing the main environmental variation across the sampling localities, 2) directly modelling the response of every collected harvestmen species to the summarized multivariate gradient by using the power and flexibility of Generalised Additive Models (GAM), 3) classifying the observed response patterns of the opilionid species and 4) comparing the ecological profiles (obtained in the previous modelling stage) with published ecological data.

METHODS

Material collected.—The present study is based on the examination of 31,639 specimens (8,314 males, 14,861 females, 8,464 juveniles) from 22 species and subspecies (see the number of each species caught in legend of Fig. 3), collected by the senior author in the period 28 February 1987–28 April 1989 in the region of Vitosha Mountain (peak Cherni Vrah: UTM FN81, N 42°33′48.9″, E 23°16′45.2″, 2290 m). Four species recorded from the area of the mountain (Staręga 1976; Mitov 2000; Stoyanov & Mitov 2004) are not included in the present analysis. These are: *Dicranolasma scabrum* (Herbst 1799), *Histri-costoma drenskii* Kratochvíl 1958, *Opilio parietinus* (De Geer 1778), and *Rafalskia olympica* (Kulczyński 1903). The former three species were absent from pitfall trap samples or were represented by only a few ($n < 10$) individuals, while the latter species has not been recorded from Vitosha Mountain since the original record of Staręga (1976). The collected material is in the opilionid collection of Plamen Mitov.

Sampling.—Altogether 653 pitfall traps (plastic buckets with rim diameter 10 cm and 12 cm height), filled with 4% formalin solution were used. The traps were placed 5 m apart, on a zig-zag line through 54 sampling localities, at elevations between 750 and 2290 m (the latter is the maximum elevation for this dome-like mountain), and at intervals between 200 and 500 m (depending on the relief). All major habitat types (approximately 40% of the habitats, according to Dr. Rosen Tsonev, pers. comm.) were sampled during the sampling program that covered the whole area (278 km²) of Vitosha Mountain. Samples were collected monthly. For further details on the sampling scheme see Mitov (1996).

Environmental data.—At each sampling

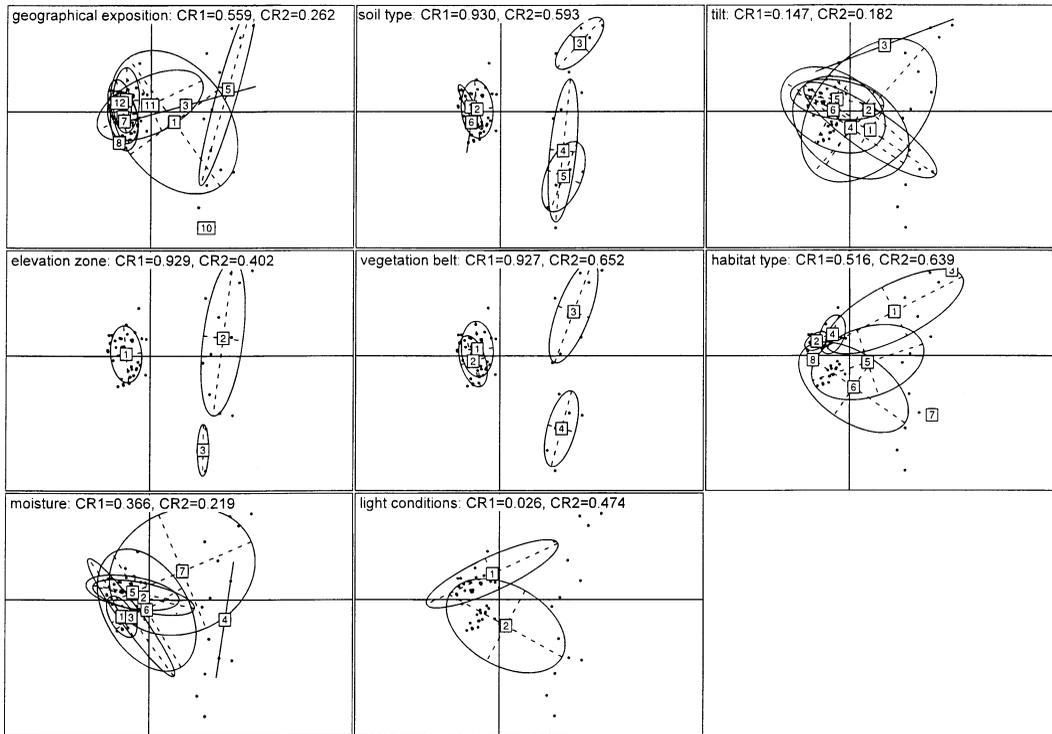


Figure 1.—Ordination diagram of the Multiple Correspondence Analysis (MCA) of the full habitat by environmental variables matrix. The first axis summarizes 11.6%, the second = 9.0% of the variability. Dots represent the sampling localities; environmental variables are shown in Table 1, ellipses visualize the spread of environmental variable modalities, CR1 and CR2 are the correlation ratios of each variable related to the first and second ordination axis.

locality the following environmental variables were measured and recorded (see Table 1): elevational (climatic) zone (3 classes, ordered; classification in Hubenov 1990), geographical exposition (12 classes, ordered) measured with compass, habitat type (8 classes), humidity (7 classes, ordered; based on indicator plants according to Nedyalkov 1998), light conditions (2 classes, ordered; based on habitat type), vegetation belt (4 classes; classification in Hubenov 1990), soil type (6 classes; classification in Chucheva 1983), and tilt (6 classes, ordered; classification in Chucheva 1983) measured with an standard plastic angle meter.

Data analyses.—The following procedure was used for modelling: 1) a Multiple Correspondence Analysis (MCA, Tenenhaus & Young 1985) was performed on the localities by environmental variables matrix to obtain a low-dimensional representation of the data structure; 2) the resulting sample ordi-

nation space (2 retained axes) was overlaid with the fitted Generalized Additive Model (GAM) surface of opilionid species abundance at the ordinated sampling sites, where the poisson error distribution and logarithmic “link function” were used for fitting. The advantage of using GAMs for the modelling is, that it is especially powerful in modelling data with non-normal error distributions (Hastie & Tibshirani 1990; Wood 2000), and that one does not have to assume a particular (unimodal or linear) response of species abundance along the environmental gradient, and thus the exploratory phase of the investigation is more flexible.

As only 9 harvestmen species were more widespread through the area of Vitosha Mountain, after modelling their abundance the site by environmental variables matrix was reduced to increase the resolution when modelling the data for the rest of the opilionid species. Fourteen high-mountain sites (in the

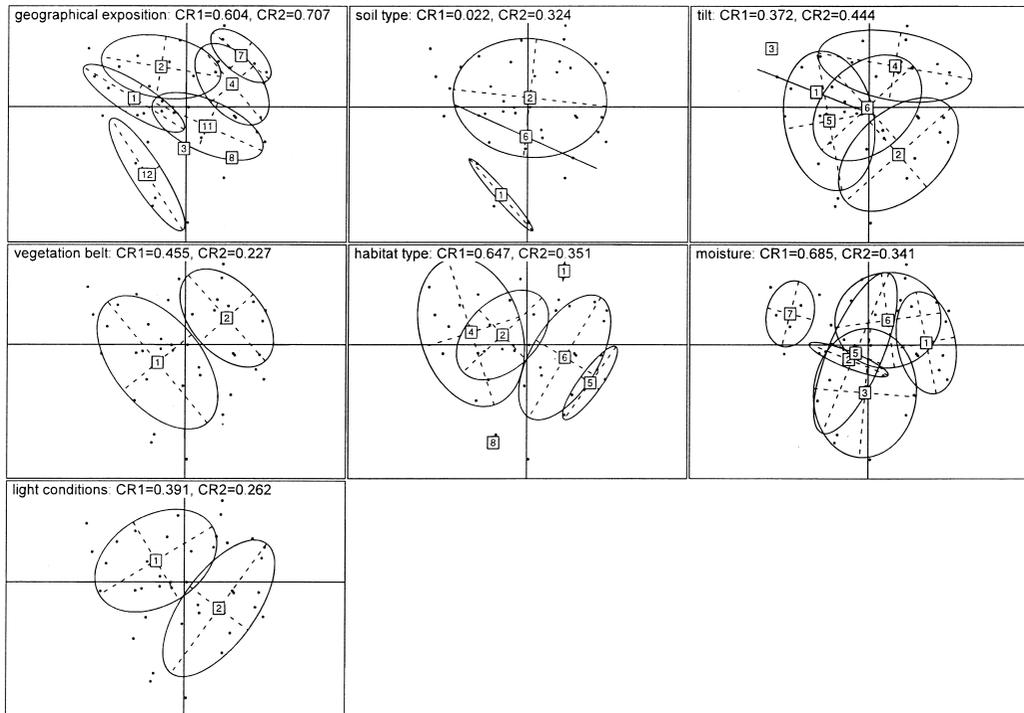


Figure 2.—Ordination diagram of the Multiple Correspondence Analysis (MCA) of the reduced habitat by environmental variables matrix (the high-mountain sites excluded). The first axis summarizes 12.2%, the second = 10.2% of the variability. Dots represent the sampling localities. For the environmental variable modalities see Table 1, ellipses visualize the spread of environmental variable modalities, CR1 and CR2 are the correlation ratios of each variable related to the first and second ordination axis.

right half of Fig. 1) were removed, in order to exclude the sites where the rest of opilionid species (13) were not (or only occasionally) present. The resulting matrix (Fig. 2) was again subjected to MCA to obtain the sampling site ordination, over which the GAM surface-fitting procedure for the remaining (i.e. those restricted to the low-mountain zone) species was applied again. All computations were performed in the R statistical language and environment (Ihaka & Gentleman 1996), using the *ade4* (Chessel et al. 2004), *mgcv* (Wood 2000), and *akima* (Akima 1978) libraries.

RESULTS

Environmental gradients.—The MCA on the sampling site by environmental variable matrix shows a strong separation of the low-mountain from the high-mountain zone (including the a priori defined middle-mountain zone, cf. “METHODS”) along the first ordi-

nation axis (see Fig. 1, “elevational zone”). The environmental variables with high correlation ratio with this axis (and thus enabling a good separation of the sampling sites along that axis) also include soil type, vegetation belt (both presenting a structure very similar to that of the elevational zone), and exposition. Most strongly associated with the second ordination axis are the following variables: vegetation belt, habitat type, soil type, and light conditions (Fig. 1). The similar patterns of soil type, elevational zone and vegetation belt are due to strong interdependence between these factors.

When analyzing the reduced sites by environmental variables matrix (Fig. 2), a not so abrupt (and hence more complex) gradient is apparent. Its first axis is mainly determined by the moisture gradient, the habitat type, and exposition, while the exposition, tilt, habitat and moisture (both similarly important) summarize the main variation along the second or-

Table 1.—Environmental variables measured at each sampling locality.

Variable	Classes
Elevational zone	1) low- (up to 1450 m), 2) middle- (1450–1850 m), 3) high-mountain zone (above 1850 m, max. 2290 m)
Geographical exposition	1) N, 2) NNE, 3) NE, 4) ENE, 5) E, 6) SE, 7) SSE, 8) S, 9) SW, 10) WSW, 11) W, 12) NNW
Habitat type	1) coniferous forests, 2) deciduous forests, 3) rivulet-bank in coniferous forests, 4) rivulet-bank in deciduous forests, 5) rivulet-bank through meadows, 6) meadows, 7) peat moss bogs, 8) forest-glades
Humidity	1) dry, 2) dry-mesophilous, 3) dry-fresh, 4) mesophilous-fresh, 5) fresh, 6) fresh-moist, 7) moist
Light conditions	1) dark, 2) light
Vegetation belt	1) <i>Quercus-Carpinus</i> , 2) <i>Fagus</i> , 3) coniferous, 4) subalpine
Soil type	1) Chromic Luvisols, 2) Distric Cambisols, 3) Humic Cambisols, 4) Orthic Umbrosols, 5) Rendzic Leptosols, 6) Histic Umbrosols
Tilt	1) 0–5°, 2) 6–10°, 3) 11–20°, 4) 21–30°, 5) 31–40°, 6) 41–50°

dination axis (see the correlation ratios in Fig. 2).

Modelled ecological profiles.—As evident from the distribution plots (Fig. 3), the distribution-patterns of the Opiliones from Vitosha Mountain may be classified in two groups. The first one contains species with region-wide distribution (indicated by the spread of lines that connect the sampling sites where a species has been sampled): *Pyza bosnica* (Roewer 1919), *Paranemastoma radewi* (Roewer 1926), *Paranemastoma aurigerum ryla* (Roewer 1951), *Phalangium opilio* Linnaeus 1758, *Rilaena* cf. *serbica* Karaman 1992, *Lophopilio palpinalis* (Herbst 1799), *Lacinius horridus* (Panzer 1794), *Mitopus morio* (Fabricius 1779), and *Leiobunum rumelicum* Šilhavý 1965. The second group include opilionid species restricted more or less to the low-mountain zone (the compact cluster, located left of the main vertical axis on Fig. 3). These are *Mitostoma chrysomelas* (Hermann 1804), *Carinostoma ornatum* (Hadži 1940), *Trogulus tricarinatus* (Linnaeus 1767), *T. clo-sanicus* Avram 1971, *Opilio saxatilis* C. L. Koch 1839, *O. ruzickai* Šilhavý 1938, *O. dinaricus* Šilhavý 1938, *Rilaena balcanica* Šilhavý 1965, *Zachaeus crista* (Brullé 1832), *Z. anatolicus* (Kulczyński, 1903), *Lacinius dentiger* (C.L. Koch 1847), *L. ephippiatus* (C.L. Koch 1835), *Odiellus lendli* (Sørensen 1894).

The fitted GAM surfaces for some of the members of the first group mentioned above do not show any prominent optimum within the study area, as for example *Pyza bosnica*,

Paranemastoma radewi, *Lophopilio palpinalis*, and *Mitopus morio* (Fig. 4). These species increase their abundance towards the margin of the scatterplot more or less linearly. The first mentioned species has its maximum abundance in the low-mountain zone as well as in the coniferous forest habitats (in the middle-mountain zone); the second species tends to occur more massively in deciduous forests (in the low-mountain zone), and the latter two reach highest numbers in the middle- and high-mountain zones respectively. *Leiobunum rumelicum* is mainly distributed in forest habitats (predominantly in the low-mountain zone and several occupied localities in the middle-mountain zone). *Rilaena* cf. *serbica* and *Phalangium opilio* seem to prefer middle-mountain open habitats (where a well defined peak may be observed); a similar pattern is also displayed by *Paranemastoma aurigerum ryla*, but the peak is not so prominent. Finally *Lacinius horridus* shows a clearly bimodal distribution pattern, showing a prominent peak in forests of the low-mountain zone and increasing at the same time its abundance towards open habitats in the middle-mountain zone.

From the predominantly low-mountain harvestmen species, *Zachaeus crista* (Fig. 5) and *Trogulus tricarinatus* (not shown) are more or less evenly distributed within the zone. *Rilaena balcanica* (Fig. 5), *O. dinaricus*, and *Opilio ruzickai* (both not shown) are clearly associated with forests locations in the oak-hornbeam vegetation zone. The modelled responses of *Carinostoma ornatum* and *Opilio*

saxatilis (Fig. 5) show a clear preferendum (peak) towards relatively dry and open habitats, the peak of the latter species is more towards open and dryer (and not so slanted) stations (cf. the habitat characteristics distribution on Fig. 2).

In contrast to the previously mentioned species, the following harvestmen do not show a pronounced optimum in their response. *Lacinius dentiger* (Fig. 5) and *Lacinius ephippiatus* (not shown) demonstrate a slightly bimodal response, being strongly associated with fresh to moist slanted forest habitats in both the beech and oak-hornbeam vegetation belt (the latter species being more dependent on moisture conditions, than the former). A somewhat bimodal, but not easy interpretable response pattern may be observed on the GAM plot for *Trogulus closanicus* (Fig. 5). This species seems to be associated with fresh to moist riverside habitats in forests and fresh meadows, but due to the relatively low number of individuals collected, this pattern is not very well supported.

Finally, the abundances of three of the opilionid species: *Mitostoma chrysomelas*, *Zachaeus anatolicus* and *Odiellus lendli*, could not be modelled because of their very restricted occurrence (i.e. very low frequency and abundance of catches) on Vitosha Mountain. The last mentioned species were collected mainly on a few meadows, and while *Z. anatolicus* could be regarded as relatively rare throughout Bulgaria, *O. lendli* was locally very abundant (911 specimens come from a fresh beech forest meadow).

When focusing on the response types of congeneric opilionid species, we may observe that these species tend to display opposite trends, as for example the species of the genera *Paranemastoma* Redikorzev, 1936 (Figs. 3, 4), *Lacinius* Thorell, 1876 and *Rilaena* Šilhavý 1965. The differences are not so prominent in the responses of the *Trogulus* Latreille 1802 and *Zachaeus* C.L. Koch, 1839 species, while in species of the genus *Opilio* Herbst, 1798 only the response of *O. saxatilis* shows a trend opposite to the responses of the other species from this genus (Fig. 3).

Ecological profiles from literature data.—When examining the published ecological profiles of harvestmen species, four groups can be delimited.

1. In the first one we include species that

have repeatedly been reported to prefer moist habitats in forests. These are *Paranemastoma radewi* (Staręga 1976; Mitov 1986, 1996), *Pyza bosnica* (Staręga 1976; Mitov & Stoyanov 2004), *Paranemastoma aurigerum ryla* (see Staręga 1976), *Lophopilio palpinalis* (Pfeifer 1956; Cîrdei & Bulimar 1960; Hiebsch 1972; Weiss 1975; Staręga 1976; Martens 1978; Geyer 1983; Bliss & Tietze 1984; Müller 1984; Platen et al. 1991; Platen 1996, 2000; Platen & Broen 2002; Komposch 1997a, b, 1999; Metzen & Cölln 1998; Komposch & Gruber 2004; Mitov & Stoyanov 2004; but see above for alternative opinions) and *L. ephippiatus* (Mitov & Stoyanov 2004). Nevertheless, many European harvestmen researchers have described the latter as eurytopic (Platen et al. 1991; Platen 1996, 2000; Platen & Broen 2002; Komposch 1997a, 1999), hygrophilous (Martens 1978; Hiebsch 1978; Müller 1984; Platen et al. 1991; Karaman 1995; Komposch 1997a, 1999, 2001; Komposch & Gruber 2004), thermophilous (Pfeifer 1956), or as a montane forest species (Staręga 1976). Despite the scarce information in the literature about the ecological status of *Leioibunum rumelicum*, which only Staręga (1976) reported as a species inhabiting montane forests, we add this species to the above mentioned group.

2. According to the examined literature sources, most of the species found in the Vitosha Mountain seem to generally prefer thermophilous forests in the low-mountain zone. This group include *Rilaena* cf. *serbica* (only recently reported from Bulgaria by Mitov & Stoyanov 2004 who described it as thermophilous forest-dweller), *Lacinius horridus* (Pfeifer 1956; Staręga 1976; Martens 1978; Thaler 1979; Müller 1984; Platen et al. 1991; Weiss 1996; Karaman 1995; Metzen & Cölln 1998; Komposch 1999; Platen & Broen 2002; Komposch & Gruber 2004; Mitov & Stoyanov 2004), and *Trogulus tricarinatus* (Kolosváry 1965; Staręga 1976; Martens 1978; Platen et al. 1991; Karaman 1995; Weiss 1996; Komposch 1997a, 1999; Metzen & Cölln 1998; Platen 2000; Muster 2001; Platen & Broen 2002; Komposch & Gruber 2004; Mitov & Stoyanov 2004; but Komposch & Gruber (2004) question its thermophily). As the representatives of genus *Zachaeus* C.L. Koch 1839 have been repeatedly classified as thermophilous (Martens 1978), it is understand-

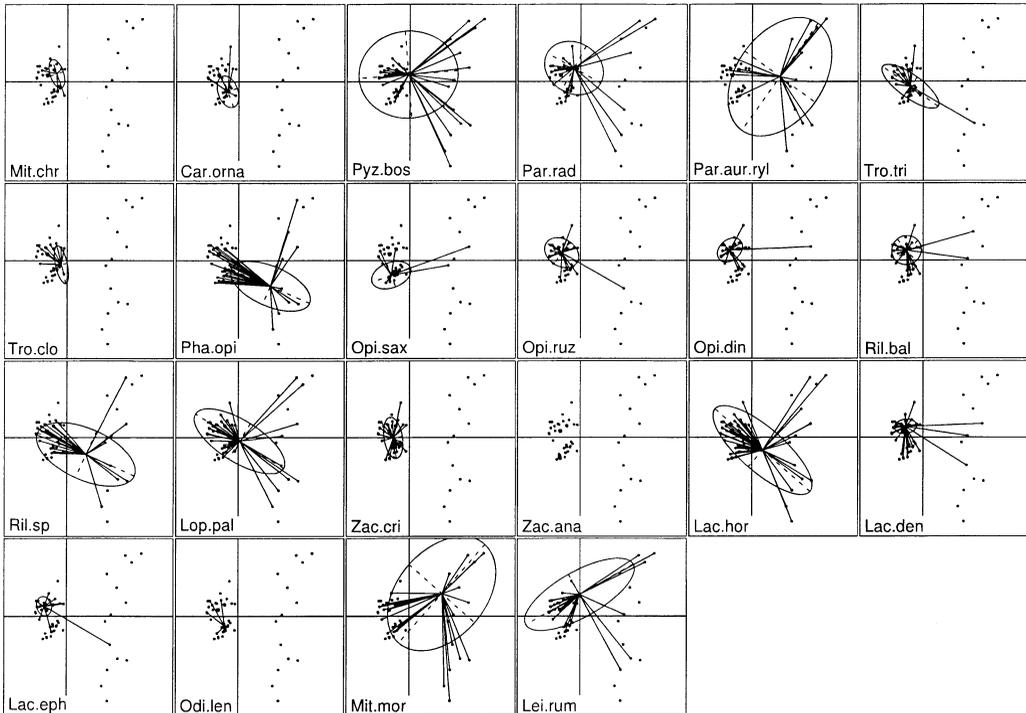


Figure 3.—Distribution plot of the Opiliones from Vitosha Mountain. The space of sampling localities (dots) is the same as in Fig. 1; lines connect samples where each species is present with the centroid of the distribution; ellipses visualize the spread of individual species occurrences. Species name abbreviations: Mit.chr (*Mitostoma chrysomelas*, $n = 17$ sampled individuals), Car.orna (*Carinostoma ornatum*, $n = 45$), Pyz.bos (*Pyza bosnica*, $n = 1844$), Par.rad (*Paranemastoma radewi*, $n = 774$), Par.aur.ryl (*P.aurigerum ryla*, $n = 318$), Tro.tri (*Trogulus tricarinatus*, $n = 89$), Tro.clo (*T. closanicus*, $n = 155$), Pha.opi (*Phalangium opilio*, $n = 2875$), Opi.sax (*Opilio saxatilis*, $n = 103$), Opi.ruz (*O. ruzickai*, $n = 76$), Opi.din (*O. dinaricus*, $n = 318$), Ril.bal (*Rilaena balcanica*, $n = 996$), Ril.sp (*R. cf. serbica*, $n = 533$), Lop.pal (*Lophopilio palpalis*, $n = 1881$), Zac.cri (*Zachaeus crista*, $n = 1431$), Zac.ana (*Z. anatolicus*, $n = 26$), Lac.hor (*Lacinius horridus*, $n = 12164$), Lac.den (*L. dentiger*, $n = 1950$), Lac.eph (*L. ephippiatus*, $n = 689$), Odi.len (*Odiellus lendli*, $n = 1002$), Mit.mor (*Mitopus morio*, $n = 4021$), Lei.rum (*Leiobunum rumelicum*, $n = 342$).

able that *Zachaeus crista* also falls into this group (Starega 1976; Weiss & Sârbu 1977; Martens 1978; Weiss 1975, 1996; Karaman 1995; Mitov 2003; Mitov & Stoyanov 2004). Here we include also *Opilio ruzickai* (Starega 1976; Komposch & Gruber 2004; Mitov & Stoyanov 2004), *Opilio dinaricus* (Komposch 1997a, 1999; Mitov & Stoyanov 2004), *Rilaena balcanica* (Starega 1976; Mitov & Stoyanov 2004) and *Lacinius dentiger* (Cîrdei & Bulimar 1960; Starega 1976; Martens 1978; Thaler 1979; Karaman 1995; Komposch 1995, 1997a, 1999; Platen & Broen 2002; Komposch & Gruber 2004; Mitov & Stoyanov 2004).

3. The third group includes harvestmen that occur in forests, as well as in open habitats.

These species have been frequently described as eurytopic, such as *Mitopus morio* (e. g. Cîrdei & Bulimar 1960; Tischler 1967; Starega 1976; Martens 1978; Geyer 1983; Müller 1984; Platen et al. 1991; Karaman 1995; Komposch 1997a,b, 1999; Metzen & Cölln 1998; Zingerle 1999, 2000; Platen 2000, Muster 2001; Platen & Broen 2002; Komposch & Gruber 2004), *Mitostoma chrysomelas* (Martens 1978; Weiss 1984, 1996; Karaman 1995; Komposch 1997a,b; Metzen & Cölln 1998; Zingerle 1999, 2000; Muster 2001; Komposch & Gruber 2004); the latter has also been described as euryphotic-hygrophilous (Hiebsch 1972) and forest hygrobiont/philic species, also inhabiting open habitats (Meijer 1972; Starega 1976; Platen et al. 1991; Platen 1996,

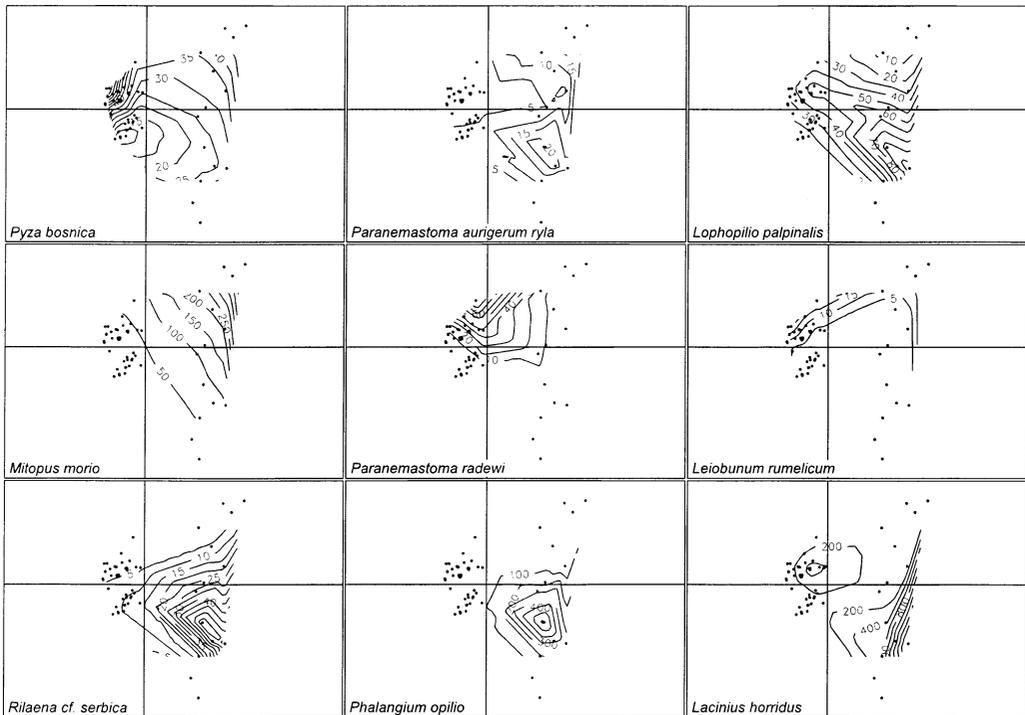


Figure 4.—GAM surface plots for the modelled abundance of harvestman species that occurred at all elevations: *Pyza bosnica*, *Paranemastoma aurigerum ryla*, *Lophopilio palpinalis*, *Mitopus morio*, *Paranemastoma radewi*, *Leiobunum rumelicum*, *Rilaena cf. serbica*, *Phalangium opilio*, *Lacinius horridus*. The space of sampling localities (dots) is the same as in Fig. 1; the isolines show the modelled abundance of each species.

2000; Platen & Broen 2002). *Carinostoma ornatum* (Staręga 1976; Mitov 1986; Karaman 1995; Mitov & Stoyanov 2004), *Trogulus clo-sanicus* (Weiss 1978, 1996; Komposch 1997a, 1999; Metzen & Cölln 1998; Mitov & Stoyanov 2004) and the thermophilous, photophilous and xerophilous *Odiellus lendli* (Staręga 1976; Weiss & Sârbu 1977; Mitov & Stoyanov 2004) are also included in this group.

4. The last three species may be listed together as harvestmen characteristic of open habitats. This group contains the relatively well known, ecologically widely adapted, photophilous, and thermophilous species such as *Phalangium opilio* and *Opilio saxatilis* (Pfeifer 1956; Kolosváry 1965, 1966a,b; Staręga 1976; Weiss & Sârbu 1977; Hiebsch 1978; Czechowski et al. 1981; Klimeš 1987; Kuschka 1991; Platen et al. 1991; Platen & Broen 2002; Karaman 1995; Weiss 1996; Komposch 1997a, 1999, 2001, 2004; Metzen & Cölln 1998; Mitov 2003; Komposch & Gruber 2004; Mitov & Stoyanov 2004), as

well as *Zachaeus anatolicus*, a Balkan sub-endemic (Mitov 2004), that may also be included here, based on a single report about its thermophilic nature (Mitov 2001).

DISCUSSION

According to the summarized literature data, habitat type and moisture are the most important factors for the ecological classification of the opilionid species. Our data, gathered from a study at a Bulgarian mountain, demonstrated that the main factor responsible for determining the ecological profiles of the harvestmen is elevation. But since elevation could not be regarded as a physiologically active factor *per se*, it may be suggested that elevational biotic (e.g. the decrease of productivity) or abiotic (e.g. low amount of available microhabitats, harsher climatic conditions) correlates, or even an unmeasured environmental parameter, would rather be the immediate ecological component acting upon the harvestmen. However, the habitat type and

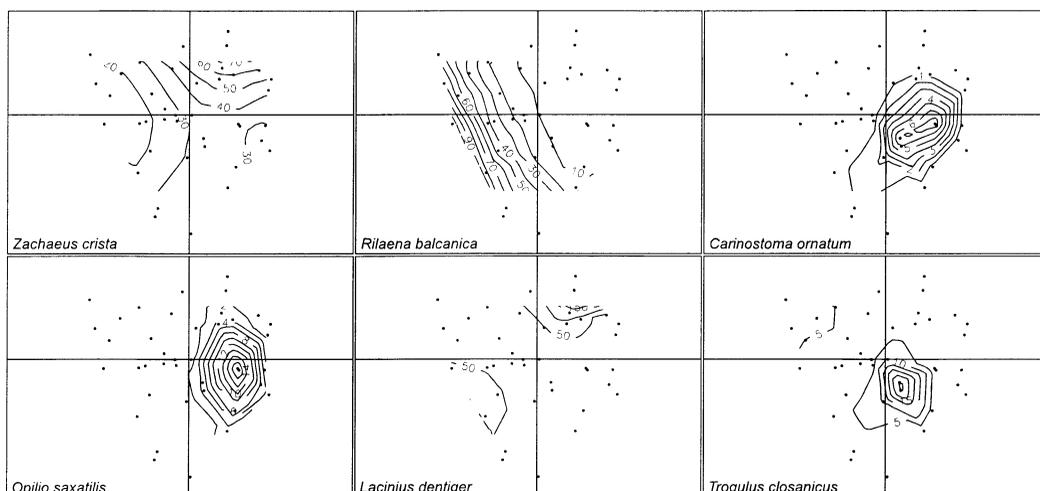


Figure 5.—GAM surface plots for the modelled abundance of harvestman species that occurred only at low-elevations localities: *Zachaeus crista*, *Rilaena balcanica*, *Carinostoma ornatum*, *Opilio saxatilis*, *Lacinius dentiger*, *Trogulus closanicus*. The space of sampling localities (dots) is the same as in Fig. 2; the isolines show the modelled abundance of each species.

moisture turned out to be of some importance for the species in the low-mountain zone of Vitosha, mainly because the habitat type depends on moisture on one hand and regulates it on the other. This observation is in concordance with the observations of Platen (pers. comm.) that in Germany most harvestmen species occur in shady and somewhat moist habitats. It might be suggested that elevation was found to be an important factor mainly because of the “mountainous” character of this study, but two further works, one on a mountain (Muster 2001; Alps) and a region-wide one (Klimeš 1997, data from the entire Czech Republic) also demonstrated the primary role of elevation for shaping the opilionid assemblages.

One particular reason for the failure of this investigation to show any strong association of the Opiliones with factors other than elevation, could be a result of the very complex environmental matrix obtained in this study. The habitat parameter that showed the best spread among the sampled localities was the elevation (and its correlates such as vegetation belt and soil type; see Figs. 1, 2). The other measured environmental parameters do not show such a broad variation among sampling units, and thus may not contribute significantly to their discrimination. Consequently, when modelled over the ordination plane, the

response of individual species could not be clearly associated with environmental factors that do not demonstrate large variation across the investigated area, especially when these responses do not show any pronounced optima at factor centroids. Another reason could be the dependence of harvestmen on various structures or conditions occurring within a specific habitat (and not on the habitat itself). Since we have not investigated microhabitat structures, this question should remain open until a study focused on within-habitat (microhabitat) structures is conducted.

In contrast to the mostly unnuanced and undiversified classifications found in the literature, is the finding that different species show quite different response-types towards the environmental parameters. This fact could not be discovered by the modelling studies cited above (Klimeš 1997; Muster 2001), since these have employed the modelling technique of choice without verifying its basic assumptions (i. e. the unimodal response of species). We found that in fact the minority of the harvestmen species from Vitosha Mountain had a unimodal distribution with a clear optimum (or preferendum) throughout the studied area. This linear response may be due to the investigations following a gradient of elevation, and because some species have made their niche at a certain elevation to avoid compe-

tition and/or unfavourable environmental conditions. As Platen pointed out (pers. comm.), even in a lowland opilions may display unimodal responses along gradients of moisture and light exposure, respectively. Whether there is a bimodal response in some species can be precisely decided in laboratory experiments, but it may be suggested that it would be of rare occurrence in Opiliones because of their strong dependence on humidity. In this situation it may be argued that an even more variable environmental matrix (i.e. with broader amplitude of environmental conditions, or including more measured environmental variables) and/or specially designed laboratory experiments should be used for refining the delineated ecological profiles, as well as for allowing the observation of potential uni- and bimodal responses of harvestmen species.

Another important information that emerged from this study is that congeneric species are quite different in their responses towards the environmental variables. This has been repeatedly postulated by theoretical ecologists as a mechanism for minimizing the potential competition (e.g. Begon et al. 1996; Giller 1984), and we suggest that this could be valid also for the Opiliones from Vitosha Mountain.

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