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Phenology of Opiliones on an altitudinal gradient on Lefka Ori Mountains, Crete, Greece

Maria Chatzaki: Department of Molecular Biology and Genetics, Democritus University of Thrace, Dragana, 68100, Alexandroupolis, Greece. E-mail: maria.chatzaki@gmail.com

Petros Lymberakis: Natural History Museum of Crete, University of Crete, P.O. Box 2208, 71409 Irakleio, Greece

Plamen Mitov: Department of Zoology and Anthropology, Faculty of Biology, University of Sofia, 8, Dragan Tsankov Boulevard, 1164 Sofia, Bulgaria

Moysis Mylonas: Natural History Museum of Crete, Department of Biology, University of Crete, P.O. Box 2208, 71409 Irakleio, Greece

Abstract. The harvestman fauna was studied along an altitudinal gradient on the southern slope of Lefka Ori Mountains, Crete, Greece for one year. Four sampling areas were defined at 800, 1200, 1600, and 2000 m elevation and they were sampled with pitfall traps that were emptied at monthly intervals. In total, six species were collected: *Histricostoma creticum* (Roewer 1927), *Lacinius insularis* Roewer 1923, *Graecophalangium cretaeum* Martens 1966, *Opilio insulae* Roewer 1956, *Rafalskia cretica* (Roewer 1923) and *Leiobunum ghigii* Di Caporiacco 1929. Species richness was the same (5 spp.) at the three lower zones and then declined to three species at 2000 m. Catches were more than double at this elevation. Differences of phenological patterns were observed among species and among altitudinal zones within the same species. High activity during spring and autumn and a summer recession were characteristic of most taxa. Opiliones did not seem strongly affected by the severe harshness of climatic conditions at higher elevations, as observed in other taxa, indicating a strong physiological tolerance and/or behavioral adaptation in order to withstand environmental stress.

Keywords: Elevation, harvestmen, Mediterranean, pitfall traps, seasonal variation

Mountain ecology has long been the focus of interest for many plant and animal ecologists. Mani (1968) compiled the earlier entomological literature of the alpine zone, which consists mainly of anecdotal, casual, or incidental observations. The lack of knowledge on quantitative and functional aspects of the soil fauna of Mediterranean-type ecosystems has been noted by Di Castri & Vitali-Di Castri (1981). However an effort has been made to try to clarify patterns of ecological variation in this kind of ecosystems in Greece. Stamou et al. (1984) studied the soil macrofauna succession in Mt. Olympus and Legakis (1986) analyzed the arthropod soil fauna of Mt. Hymettos. Despite their contribution to the knowledge of ecological variation of the fauna in Mediterranean-type ecosystems, these studies covered few taxonomic groups and did not account for seasonal variation of the fauna. Sfenthourakis (1992) gave a clearer picture of the variation of isopod assemblages along altitudinal gradients in three mountain systems of Greece. Lymberakis et al. (2003) discussed the altitudinal variation of Oniscidean communities and Chatzaki et al. (2005a) presented the variation of spider communities along altitudinal gradients on the island of Crete, Greece, as far as both composition and activity on a year-long basis are concerned. The phenology of the same group is presented in a separate paper (Chatzaki et al. 2005b).

Studies on the Opiliones of Crete have been predominantly faunistic and taxonomic. Only the work of Martens (1966) contains some phenological and chorological notes concerning the opilionid fauna of the island. As a whole, publications about the biology, ecology, and zoogeography of the group on Crete are lacking.

In view of this, the present paper is the first that concentrates on the comparison of the phenology of Opiliones at different elevations, as well as on the seasonal and altitudinal variation in species composition in Lefka Ori (White Mountains) on Crete. Lefka Ori is one of the most important insular mountain systems of the Mediterranean region, because of its high elevations, the large area it covers and its unique topography and climate (see climate paragraph in Methods).

The results presented here may serve as a basis for further comparison of the phenological peculiarities of the Opiliones in the region, as well as for the evaluation and analysis of the adaptive strategies of the endemics and their related species in other parts of the Balkan Peninsula.

METHODS

Description of the study area.—The Lefka Ori mountain system, situated at the western part of the island, is the most massive mountain range of Crete, including 56 peaks over 2000 m, the highest of which reaches an elevation of 2453 m. The study was carried out on the southern slope of Lefka Ori, just above the plateau of Anopolis found at ca 600 m (Fig. 1). Four sampling sites were selected, according to the main vegetation types, along the altitudinal gradient from 800 m to 2000 m:

1. An old mature forest of *Pinus brutia* Ten. at 800 m above sea level (a.s.l.) (35°14′N, 24°5′E), with very little understory, consisting mainly of *Quercus coccifera* L. shrubs and phrygana species, such as *Euphorbia acanthothamnos* Heldr. & Sart. ex Boiss., *Sarcopoterium spinosum* (L.), *Verbascum spinosum* L. and *Drimia maritima* (L.).
2. A *Cupressus sempervirens* L. mature forest at 1200 m a.s.l. (35°15′N, 24°6′E), composed mainly of *Cupressus sempervirens*, *Quercus coccifera* and a few *Acer sempervirens* L. trees. The understory is practically absent in this vegetation type.
3. A plateau immediately over the timberline at 1600 m a.s.l. (35°16′N, 24°5′E), partially covered with crawling

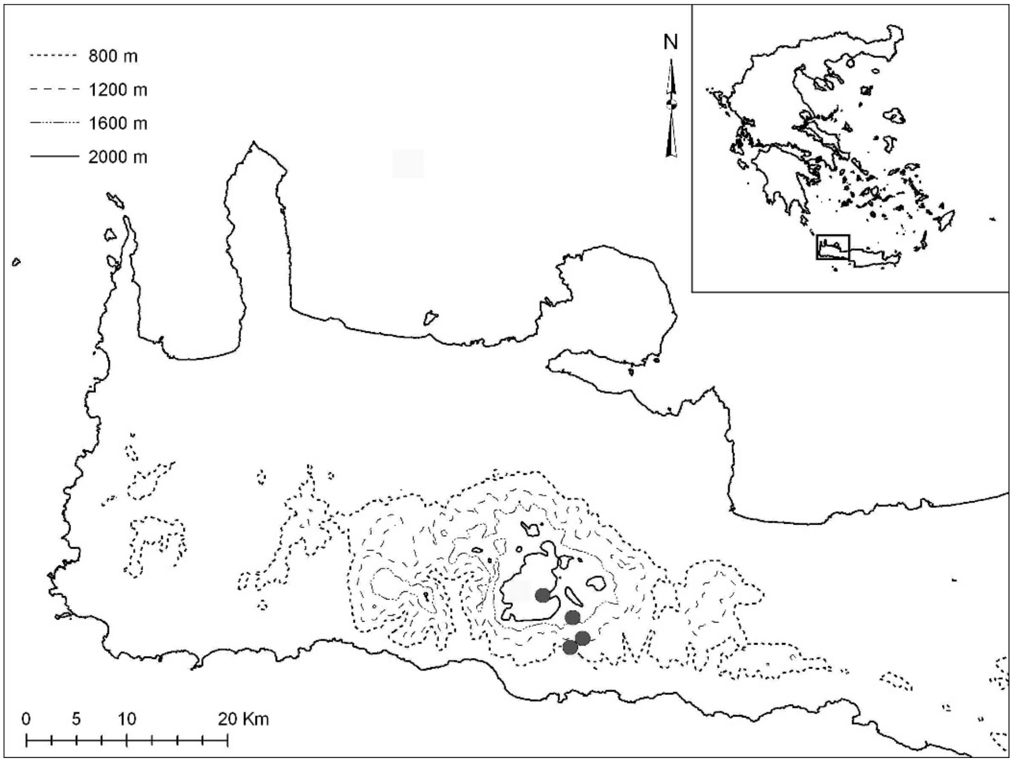

Figure 1.—Western end of Crete with collection sites. Inset: Greece.

scrubs of *Juniperus oxycedrus* L. subsp. *oxycedrus* and *Berberis cretica* L., accompanied by *Prunus prostrata* Labill., *Rhamnus saxatilis* Jacq. subsp. *prunifolia* (Sm), *Acantholimon ulicinum* (Willd. ex Schult.), *Satureja spinosa* L. and *Anchusa caespitosa* Lam.

4. A rocky site at 2000 m a.s.l. (35°17′N, 24°3′E), where the dominant scrub plants are: *Berberis cretica*, *Prunus prostrata*, *Astragalus angustifolious* Lam., and *Satureja spinosa*. Plants are largely restricted to areas offering wind shelter.

The area, as the whole of the island, is a karstic landscape. The ground is largely covered by stones and rocks that provide shelters for ground living animals. Human presence in the area dates from antiquity. For the last two centuries, but especially at present, intense grazing by sheep and goats takes place over the entire area. A main effect of overgrazing and the consequent trampling of the soil is that densities of most arthropod taxa have been reduced (Legakis 1986).

Climate.—The climate of Crete is typical Mediterranean with 5–7 mo of arid, hot and dry summers, alternating with shorter periods of rainy, mild winters. There are not sufficient meteorological data, especially for the high mountains. Mean annual temperatures fall 6° C per 1000 m rise in elevation (Grove et al. 1991). The range of temperatures is much narrower near the coast than in the mountains, due to the more maritime character of the former (Strid et al. 1995). Although there are no records of the precipitation above 900 m, Rackham & Moody (1996) estimated that at the top of Lefka Ori the annual precipitation must be as high as 2000 mm. In southern Lefka Ori, snow above 1400 m can be several meters high, but the water disappears into the porous crystalline limestone immediately after the snow melts in May. Bonnefont (1972) estimated that snow cover lasts in Crete for 2–3 mo at 1500 m and for 5–6 mo at 2000 m. Over 2000 m, the snow cover lasts generally from November to May and then melts progressively. Small, localized spots can persist until August. During the summer months, the lower atmospheric pressure and the lack of trees combined with other physical characteristics (strong winds, thin soils, large proportion of precipitation as snow), favor high insolation and create dry and hot conditions (Shanks 1956; Mani 1990). This harsh landscape (because of snow cover in winter and high aridity in summer) forms the "High Desert" of the Lefka Ori highlands, a term coined by Rackham & Moody (1996) to describe a unique environment that does not exist to such extreme in any other Mediterranean mountain.

Sampling.—Harvestmen were collected by pitfall trapping. Forty plastic cups (10 cm depth × 7 cm diam.) were used per site. Though these dimensions are rather small, traps were capable of catching large arthropods (scorpions, large spiders, centipedes), and even lizards. Traps were placed in a straight-line ca 3 m apart. Undiluted ethylene glycol was used as a preservative. To diminish passive filling of the traps with organic matter and water, as well as predation from larger animals and vandalism, they were partially covered with stones, without reducing access to them by the animals. Traps were emptied at approximately 30-day intervals from August 1990 to March 1992. However, the results presented here include data from one full collecting year (March 1991 to February 1992), since data from the other years did not deviate from the results obtained from the main collecting

Table 1.—Species overall presence and total activity (transformed into number of individuals per 100 trap-days) at different elevations of Lefka Ori Mountain, Crete.

Species	Elevation			
	800 m	1200 m	1600 m	2000 m
Lacinius insularis	2.82		21.06	31.94
Opilio insulae	6.48	20.97	6.56	32.10
Graecophalangium cretaeum	4.32	5.73	6.01	9.70
Rafalskia cretica	13.00	6.53	0.84	
Histricostoma creticum	0.36	0.16		
Leiobunum ghigii		1.27	0.26	
Total	26.98	34.66	34.73	73.74

year. In the phenology graphs the last two months are presented jointly (J–F) because there was no intermediate emptying of the traps.

Data analysis.—Opiliones were identified by P. Mitov. Vouchers are deposited at the Natural History Museum of the University of Crete and some are kept in the private collection of P. Mitov.

As some traps were destroyed or the number of collecting days per sampling period was not equal, sampling effort was unequal too. In order to render the data from four sites and eleven sampling periods comparable, catches from each sample were transformed into catches per 100 trap-days.

RESULTS

Descriptive analysis and correlation.—Six species, belonging to the families Phalangiidae (4 spp.), Nemastomatidae (1 sp.) and Sclerosomatidae (1 sp.) and represented by 2226 specimens were collected. Species are: *Histricostoma creticum* (Roewer 1927), *Lacinius insularis* Roewer 1923, *Graecophalangium cretaeum* Martens 1966, *Opilio insulae* Roewer 1956, *Rafalskia cretica* (Roewer 1923) (=*Metaplatybunus rhodiensis* Roewer 1924), and *Leiobunum ghigii* Di Caporiacco 1929. The latter is recorded from Crete for the first time. Two out of the three species that reach the elevation of 2000 m -*L. insularis* and *G. cretaeum*- are endemic to the island. All other species may be characterized as Ponto-Mediterranean faunistic elements (sensu De Lattin 1949, 1967).

Species overall presence and total catches at the study sites are presented in Table 1. The number of species is five at the three lower elevations and decreases to three at 2000 m. Species overall catches increase gradually from 800 to 1600 m and become highest (more than double) at 2000 m. The qualitative and quantitative composition among the first three elevations is different.

Lacinius insularis presents statistically significant positive correlation with elevation (Pearson's coefficient $R = 0.378$, $P = 0.03$), while *Rafalskia cretica* presents significant negative correlation with increasing elevation (Pearson's coefficient $R = -0.396$, $P = 0.023$). The remaining species do not present any significant correlation with elevation.

Phenology.—The phenology of the dominant species at each site is presented in Figs. 2–5. *Lacinius insularis* was absent at the 1200 m site. Since its total catches seem to significantly increase at the two higher elevations (Table 1, Fig. 2) and sampling was equally intense at all sites, its absence from 1200 m cannot be accidental. At the other elevation, *L. insularis* shows one peak of activity in autumn, represented mainly by female individuals. This peak is shifted from November at 800 m to September at 2000 m, thus the peak of activity occurs one month earlier at each higher altitudinal zone. Juveniles become mainly active in late spring (May at 800 m and 1600 m) and then again in autumn (September–October at 800 m and November at 1600 m). At the 2000 m site juveniles become very active in June and then again in October. This probably means that individuals of this species hibernate as immatures and remain inactive for a longer period, until the following summer when they mature (August)

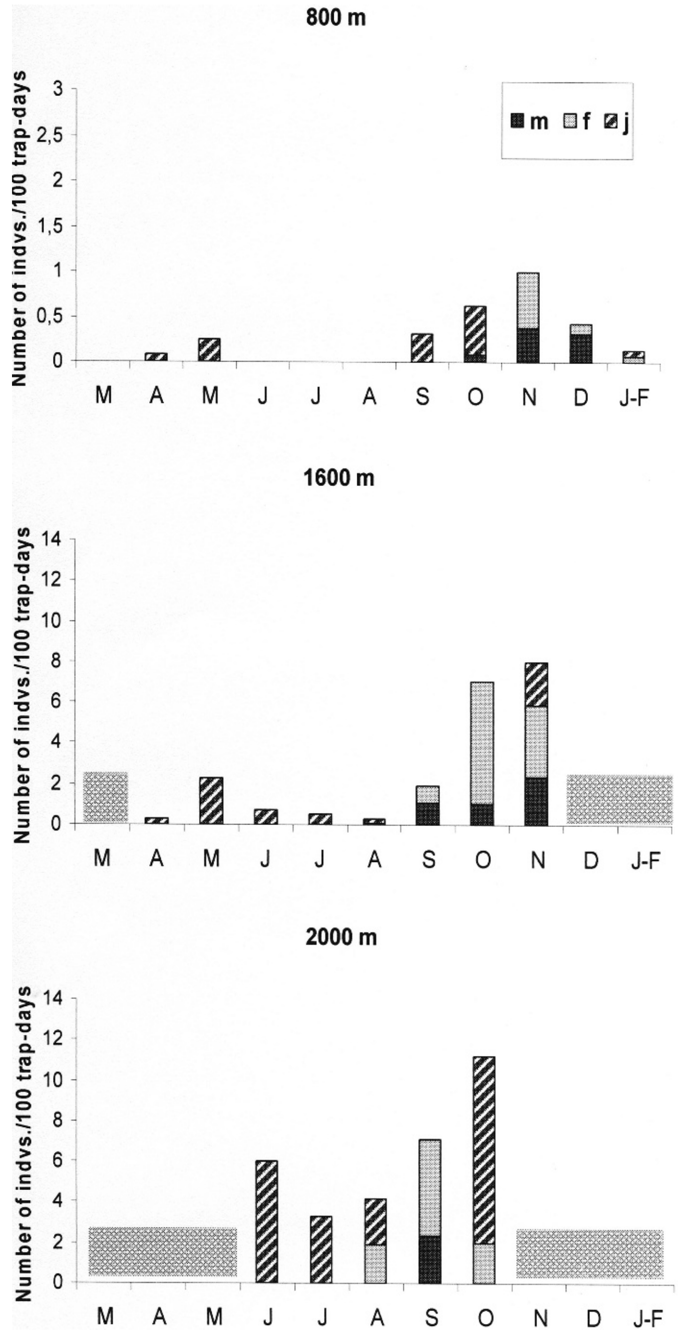

Figure 2.—Phenology of males (m), females (f) and juveniles (j) of *L. insularis* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

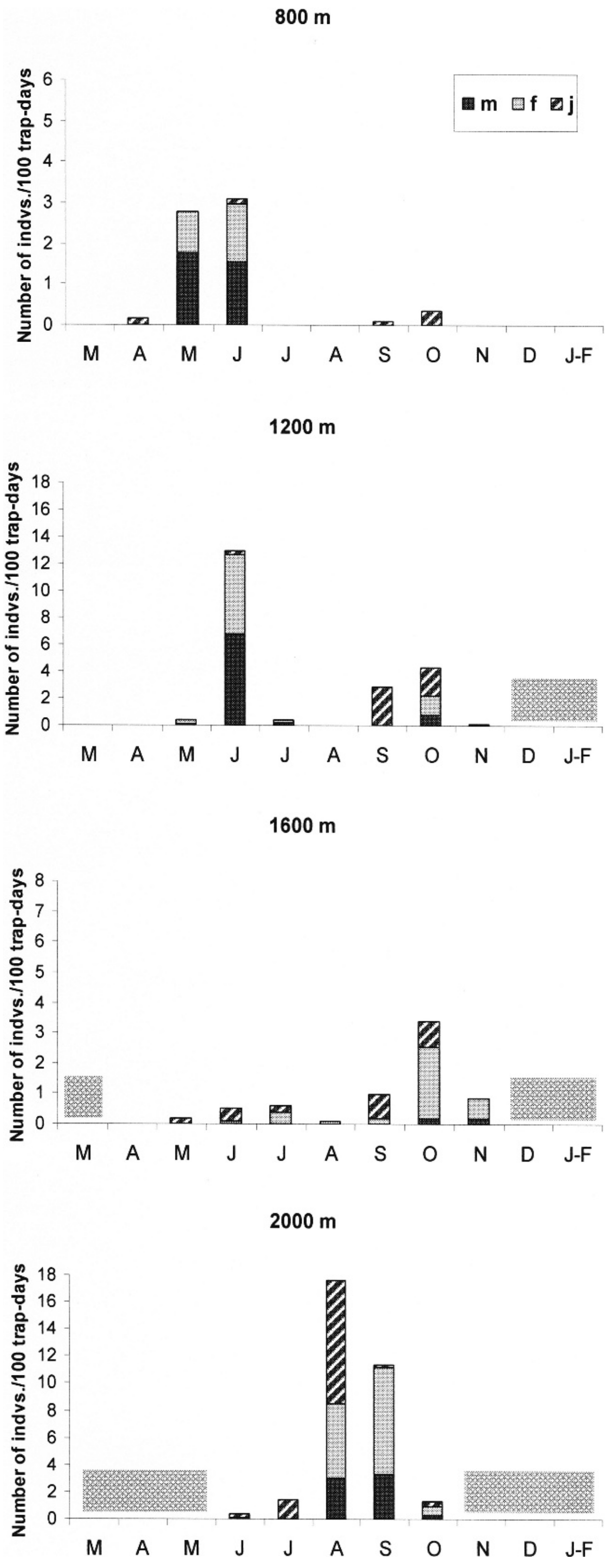

Figure 3.—Phenology of males (m), females (f) and juveniles (j) of *O. insulae* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

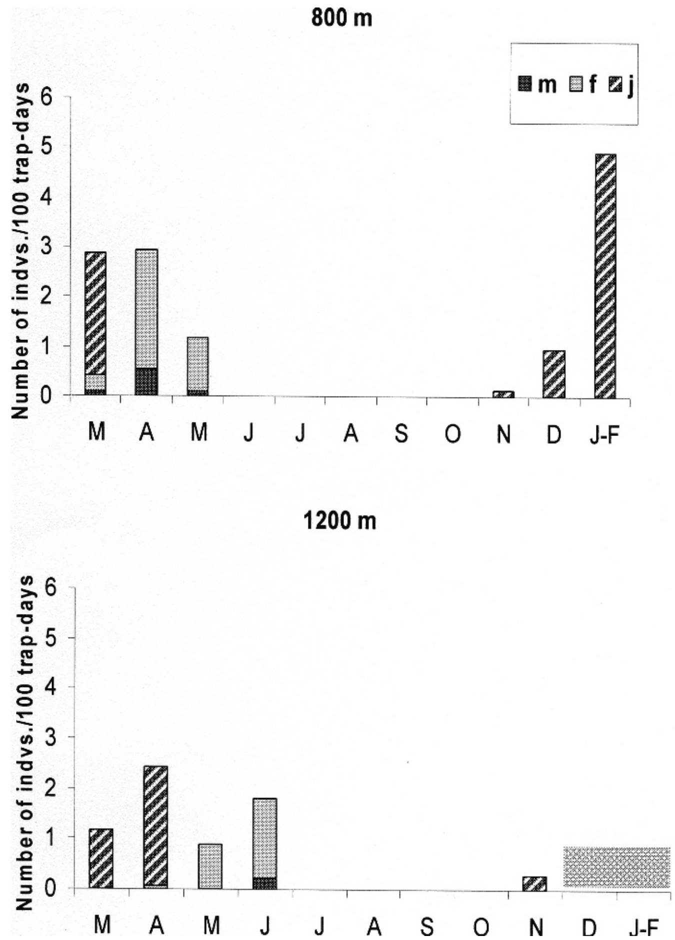

Figure 4.—Phenology of males (m), females (f) and juveniles (j) of *R. cretica* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

and are ready to reproduce in September–October. Activity under the snow cannot be excluded, but is not demonstrated by the present data.

Opilio insulae presents a clearer phenological plasticity along the altitudinal gradient (Fig. 3). At the two lower elevations it presents a peak of activity in May–June, while at the two higher elevations it presents autumn peaks, in October at 1600 m and in August–September at 2000 m. At the first three elevations, juveniles present higher activity during September–October and at 2000 m during August.

Rafalskia cretica presents an early or mid spring peak of activity (Fig. 4), thus almost avoiding *O. insulae* and *L. insularis*. Very few immature individuals were found at the 1600 m site and none at 2000 m. At the two lower elevations the peaks of adult catches are shifted from April–May at 800 m to May–June at 1200 m, while immatures are active for a longer period at 800 m (December–March) than at 1200 m (March–April).

In a similar pattern, *G. cretaeum* presents a peak in March–April at 800/1200 m which is shifted towards April–May at 1600 m (Fig. 5). Interestingly at 2000 m there are two almost equal peaks of activity of all stages simultaneously present, one in June and another one in October. Although this might indicate a double generation per year or overlapping

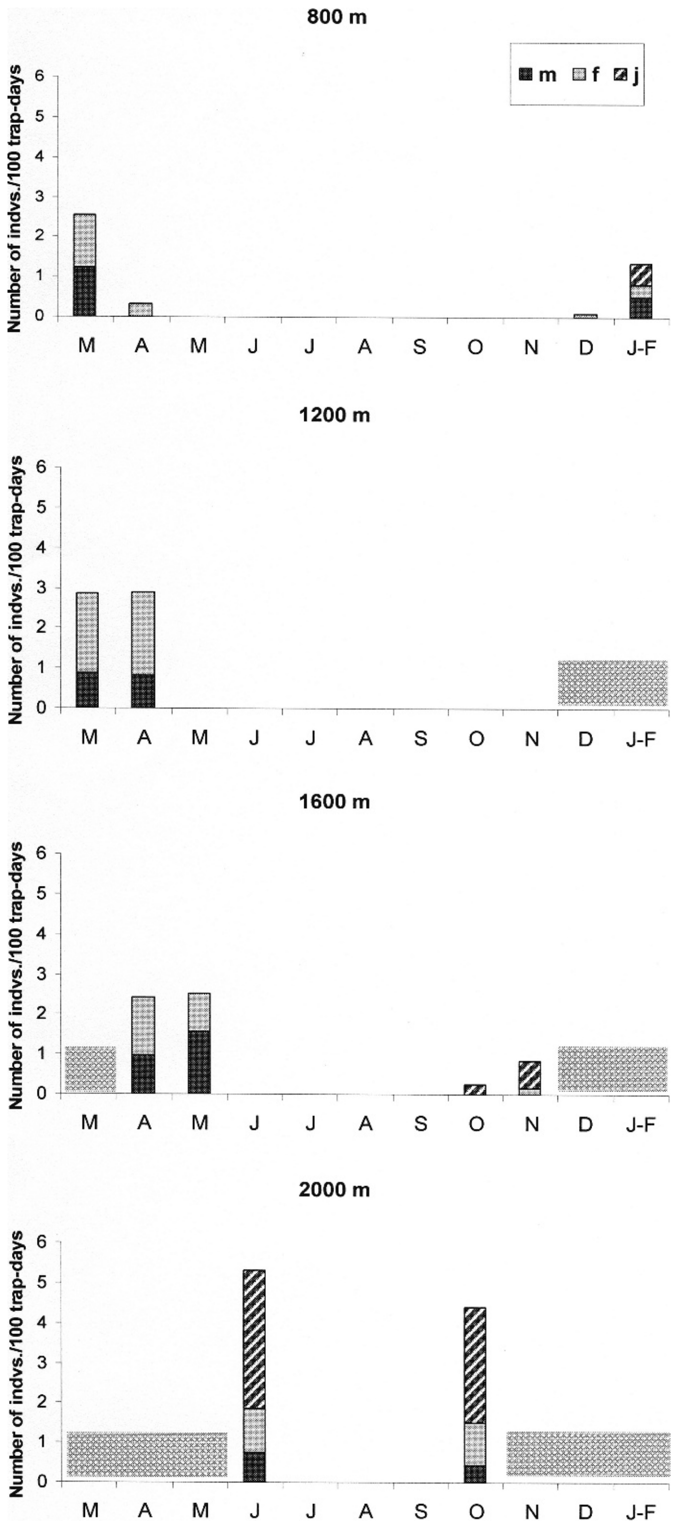

Figure 5.—Phenology of males (m), females (f) and juveniles (j) of *G. cretaeum* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

generations, the number of individuals caught is too small to allow such an interpretation. Alternatively this double peak of activity might also correspond to the same single generation of harvestmen that become active only under the most favorable conditions with optimum temperatures and humidity (i.e., June and October), while in the meantime (summer) they remain totally inactive due to their inability to tolerate the high aridity and high temperatures of this season.

Histricostoma creticum is restricted to the two lower elevations (800 and 1200 m), whereas *L. ghigii* to the two intermediate ones (1200 and 1600 m). Low numbers of both of them do not allow us any phenological interpretation. However, individuals of the former species were caught throughout the year (June, October, December and January at 800 m and April, July, November at 1200 m), while the latter species showed a tendency to be more active during autumn months (October–November).

At the two lower elevations, catches of all species cease for one (1200 m) or two (800 m) summer months (August and July–August, respectively). At the three higher elevations snow covered sampling traps for four (1200 m and 1600 m) and seven (2000 m) winter–spring months.

DISCUSSION

Phenology.—At Lefka Ori at all elevations harvestmen seem to have an annual life-cycle, as inferred from the phenological patterns (Figs. 2–5). The favorable period in which Opiliones at high elevations of Crete reach maturity is either in early autumn or in spring. Maturity lasts one to two months and is followed or preceded by a juvenile peak. In general, immature activity is expanded for a longer period within a year than mature stages, even at the highest elevations, where immature activity overlaps with that of adults (see for example *G. cretaeum* and *O. insulae* at 2000 m as extreme cases). This is common in species inhabiting high elevation habitats and signifies the shortening of biological processes within the year (Pinto-da-Rocha et al. 2007).

The phenological patterns of *L. insularis*, *R. cretica*, and *G. cretaeum* do not change along the altitudinal gradient, but their peaks of activity are shifted to one or two months later (*R. cretica* and *G. cretaeum*) or earlier (*L. insularis*) at the two higher elevations. It is important here to note that seasons are not the same at each elevation. Although lack of meteorological data allows us only to speculate, we suggest that with the rise of elevation, winter lasts longer and "squeezes out" spring and autumn. In this respect, at 2000 m October represents late autumn and June represents spring, whereas at 800 m, October and June are still very warm and dry months corresponding to "summer," taking into account the high mean temperatures encountered in both periods. Hence Opiliones find similar climatic conditions in March–April at 800 and 1200 m and in May–June at 1600 and 2000 m (i.e., *G. cretaeum*) or in October–November at 800 m and in September at 2000 m (i.e., *L. insularis*).

The case of phenological differentiation of *O. insulae* (Fig. 3) is more pronounced, changing its peaks of activity from spring (800–1200 m) to late summer/autumn (1600–2000 m). The latter pattern is one of the very few cases of late summer activity peak among all taxa studied, at all elevations. The only species that presents the same pattern of activity at Lefka Ori is *Zelotes creticus* Kulczynski 1903, an endemic spider species that belongs to the family Gnaphosidae (Chatzaki et al. 2005b). This phenomenon may indicate that at the two higher elevations both mating and egg laying occur in the same period; i.e., in late summer - beginning of autumn, while at the lower ones these processes are interrupted by the hot dry summer, during which animals remain inactive. Martens (1966) noted that the reproductive period of this harvestman in the seacoast region of Crete is from mid-April–June. This difference of phenological patterns between lowland and highland populations may possibly be justified by the climatic heterogeneity of the Cretan landscape. An alternative explanation however might be a taxonomic divergence of the species masked by morphological similarity, a phenomenon that has been observed in various taxa (e.g., Parmakelis et al. 2003 and references therein). This hypothesis remains to be further tested with molecular data.

A partitioning of the favorable periods, with peaks of activity following one another may be observed. As a result, activity periods of *R. cretica* and *G. cretaeum* never coincide with those of *O. insulae* and *L. insularis*. This seems to be the rule concerning arthropod phenology, since it has also been observed in spiders of the family Gnaphosidae (Chatzaki et al. 2005b) on Crete and in other Mediterranean regions (Urones et al. 1995) as well as in temperate ecosystems (Enders 1976; Toft 1976; Uetz 1977).

Cloudsley-Thompson (1962) places water conservation as the prime physiological problem for the survival of terrestrial invertebrates. Harvestmen are especially susceptible to water loss and this is a prime factor limiting species distributions (Hillyard & Sankey 1989; Pinto-da-Rocha et al. 2007). The fact that no harvestmen were caught for two months at 800 m and for one month at 1200 m, indicate a severe stress due to high aridity, which these animals try to overcome by ceasing their activity. Things are even more pronounced at the two higher elevations, the "High Desert" according to Rackham & Moody (1996). On one hand, snowfall and snow cover during four (1600 m) and seven months of the year, respectively, and on the other hand the extreme aridity of summer months (especially August at 2000 m), considerably restrict the suitable period for exploitation by harvestmen. A compromise between water conservation, limited time for activity, and avoidance of other species might result in the, still mysterious, mid-summer peak of activity of *O. insulae*.

Kinetic activity and species richness.—Janzen (1973), Janzen et al. (1976), Wolda (1987), and McCoy (1990) reported a decrease of the number of species and individuals of certain arthropod groups, mainly insects, along an altitudinal gradient. Almeida-Neto et al. (2006) showed a decline of both species richness and abundance of Opiliones in elevational gradients of three mountains in Brazil. Our data partially agree with the decrease in the number of species, but as far as kinetic activity of Opiliones is concerned a total increase in the number of individuals is observed, which is due to the impressive increase of three species, namely *L. insularis*, *O. insulae* and to a lesser extent *G. cretaeum*. Similarly, species of other taxa (i.e., members of the spider family Gnaphosidae (Chatzaki et al. 2005a), as well as some other families (Lycosidae, Dictynidae, Thomisidae, and Philodromidae (Chatzaki, unpublished data)) tend to reach extremely high numbers of individuals at the higher elevations of the same mountain system.

According to Hagvar et al. (1978) harvestmen is the largest group (as far as numbers of individuals are concerned) found among other predatory arthropod communities at high elevations in Norway. The difference between our results and those found by Almeida-Neto et al. (2006) as far as the abundance along elevation is concerned, may lie in the fact that the range of climatic conditions that the tropical arthropods can tolerate cannot be as wide as that tolerated by animals of the temperate zone. Therefore, Opiliones of Crete should be able to reach higher elevations (hence harsher conditions) and create denser populations there. Another point which may partly explain this difference is the methodological bias caused by the fact that the authors measured the abundance of species as revealed by hand collecting and we measured the activity/abundance in the sense of pitfall catches.

In view of the identification of the origin of the mountain harvestmen of Crete, one has to follow the paleohistory of the island formation. The mountains of Crete have a very short history dating back to the beginning of the Pliocene (Meulenkamp et al. 1994) with an estimated elevation of 2000 m since then, which was accelerated mostly during the Pleistocene (Meulenkamp 1971). This newly and rapidly formed mountain landscape gave rise to new niches on the island. Taking into consideration that Crete was isolated from the mainland since the early Pliocene (Meulenkamp et al. 1988), the only available fauna to occupy the newly formed high elevations would be the already existing lowland species.

This is true for several taxa studied until now. Studies on ground beetles (Trichas 1996), terrestrial snails (Vardinoyannis 1994) and plants (Greuter 1972) agree that life of the Cretan mountains is mainly composed of derivatives of lowland endemics and a small number of old relicts. Chatzaki et al. (2005a) found one endemic but mostly non endemic high elevation specialists and lowland species which altogether compose the main part of the arachnofauna above 1600 m. Among the 20 species of Opiliones recorded on the entire island (Giltay 1932; Roewer 1927, 1940; Martens 1965, 1966; Gruber 1998), only six are reported above 800 m at Lefka Ori mountains. Three species increase in numbers of individuals along the altitudinal gradient and dominate at higher elevations (Table 1), two of which are Cretan endemics (*L. insularis* and *G. cretaeum*). At 2000 m, the latter are the only opilionid residents together with *O. insulae*. There are no high-elevation specialists, like in ground spiders, since all three of them are also found in the lowlands of Crete (for detailed references see Roewer 1927; Giltay 1932; Martens 1966).

In conclusion, harvestmen of the high elevations of Crete show a high tolerance to the extreme climatic conditions found in these environments and do not seem to be limited by them in order to create viable populations. The six species recorded above 800 m at Lefka Ori mountains represent the most physiologically tolerant species among the lowland residents of the island and none of them is a high-elevation specialist. Most species tend to exploit the favorable period of April-June and September-October. At the higher elevations, biological cycles are compressed to a narrow period in which climatic conditions allow the animals to be active.

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