POLLINATION ECOLOGY OF LABIATAE IN A PHRYGANIC (EAST MEDITERRANEAN) ECOSYSTEM

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This study was conducted in a phryganic (East Mediterranean) ecosystem at Daphni, near Athens, Greece. The Labiatae, represented by ten species belonging to nine genera, dominate in this ecosystem type. They flower from February to July. Both flowering time and nectar quantity are related to the species ability to tolerate intense water stress. Labiatae are visited by 201 insect species. Of these, 43 are exclusively supported by the family and 37 are monotropous. Solitary bees (mainly Anthophoridiae, Megachilidiae, Halictidiae) constitute 47.3% of pollinators. The family is important in hosting specialized bees (15 species) in phrygana, particularly late in the flowering season. Labiatae species form two equally represented groups in this system; namely, the late winter-early spring (early) flowering, visited by relatively few pollinator species, and the late spring-summer (late) flowering species, visited by numerous pollinators. This temporal distinction is accompanied by different pollination profiles that include duration of anthesis, reward to pollinators, floral attractiveness, and flower character differentiation. All of these attributes are maximized in the early flowering period. This strategy suggests a mechanism for resource partitioning at a time when the pollinator resource is limited and competition for the services of pollinators is expected to be intense. Contrary to the current theory concerning cornuncopian species, the copiously rewarding flowers of Labiatae in phrygana are not those abundantly serviced by pollinators.

Phrygana, the most xeric type of the Mediterranean ecosystems (syn. tomillares in Spain, batha in Israel, garrigue in France, gariga in Italy, coastal sage in California), occupies ca. 13% of the surface of Greece (Diamantopoulos, 1983). The main feature that characterizes this ecosystem type is the seasonal dimorphism of the dominant woody plants associated with a seasonal reduction of their transpiring surface (Margaris, 1981). This is an adaptive mechanism to avoid stresses imposed by summer drought, which is the prevailing element of Mediterranean-type climate (Aschmann, 1973). Labiatae, a major family of aromatic plants, comprises a dominant component in phrygana. *Thymus capitatus* (L.) Hoffmanns. & Link, in particular, characterizes most of the phrygana of Greece, providing its characteristic fragrance.

The species of Labiatae have been recorded as predominantly bee-pollinated (van der Pijl, 1972; Stebbins, 1974; Faegri and van der Pijl, 1979). In the Mediterranean region, in particular, solitary bees constitute the majority of Labiatae pollinators (Herrera, 1987; Shmida and Du kas, 1990; Dafni, 1991). Solitary bees have a short life span of only a few weeks, which restricts them to specialize on very few plant species (Linsley, 1958; Heinrich, 1976; Eickwort and Ginsberg, 1980; Schemske, 1983). Labiatae constitute the majority of the consistent nectar producers in the Mediterranean region (Herrera, 1985; Petanidou and Vokou, 1990; Petanidou, 1991b). Therefore, they are the main source of water and nutrients for numerous native bees in an area characterized by water shortage.

The pollination ecology of Labiatae in phrygana was investigated to elucidate 1) their remarkable contribution in this ecosystem type, 2) their importance as bee hosts (solitary/specialists, in particular) and nectar/water suppliers to pollinators in an arid environment, and 3) the pollination-based relationships among them and between them and their pollinators in a community context. We focused primarily on strategies employed by sympatric species of relatively similar morphology to partition the available pollinator resource and minimize competition.

MATERIALS AND METHODS

Site—This study was conducted at Daphni, Greece, situated about 10 km west of the center of Athens, in the area of the “Diomedes Botanical Garden of the University of Athens,” reserve. Phrygana is the dominant ecosystem type of the reserve and covers 130 ha. The substrate is calcareous and stony. The study was conducted in a 30-ha section of the reserve at 135–215 m, from April 1983 to May 1987.

Plant species—Ten Labiatae species occur in the study area. These are *Lamium amplexicaule* L. ssp. *plexi-
caule, Salvia verbenaca* L., *S. triloba* L. fil., *Phlomis fruticosa* L., *Prasium majus* L., *Satureja thymbra* L., *Stachys cretica* L. ssp. *cretica, Teucrium polium* L., *Ballota acetabulosa* (L.) Bentham, and *Thymus capitatus* (L.) Hoffmanns. & Link. The features recorded were corolla color, size, depth, essential oil production, nectar amount, flower height, flower cover, flower life span, and duration of anthesis. The sample for color, size, and depth assignments consisted of 20 flowers that were collected at random from different individuals occurring in the most densely populated area of the study site for each species.

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2 Author for correspondence.
Color—Color determination was made on the basis of the Chromaticity Diagram released by the “Commission International de l’ Eclairage” (CIE) (Keller, 1983) and modified to comply with the color overlaps in the diagram. The 20 color types of the CIE diagram were combined to form seven groups: purple (purple, reddish purple, purplish red), pink (pink, purplish pink, yellowish pink), red (red, reddish orange), blue (blue, purplish blue, greenish blue), green (green, bluish green, yellowish green), yellow (yellow, yellow green, greenish yellow, orange-yellow, orange), and white. Color identification was made on site by three persons, independently presented with the 20 flower samples. Intraspecific color variation for those of pink and blue-flowering taxa never exceeded the limits of the color groups, as defined above.

Size—The planar projection of the largest surface was considered for flower-size determination (Dafni, 1991). The size measured is equal to the sum of the two maximal perpendicular axes of this surface and divided by two. Three categories were distinguished (sample average): small-sized (≤10 mm), medium-sized (11–20 mm), and large-sized (>20 mm) flowers.

Depth—Depth was measured with the aid of 10-μl Drummond micropipets. Lip junction was taken as the origin of the floral tube. Flowers were grouped into four categories (sample average): shallow (<7 mm), relatively shallow (7–10 mm), relatively deep (11–14 mm), and deep (>14 mm).

Nectar amount—The quantity of nectar was estimated by means of 10-μl Drummond micropipets. Flowers were covered with fine gauze to prevent insect access for 1 to 2 days before measurements were taken. Flowers were sampled in 2-hour intervals over the day as long as pollinators were active, at the peak of each species flowering period. For each species, nectar was measured on more than 20 flowers, except for Stachys cimetica and Salvia triloba (less than 20; Table 2). Considering the per-day nectar production, three categories were distinguished (sample average): low (<1 μl), medium (1–2 μl), and high (>2 μl) nectar producing.

Flower height—The distance from the ground of all flowers of five individuals was measured for each species, except for Satureja thymbra and Thymus capitatus. In the latter, given the high number of flowers per individual and the round shape of the plant, 20 flowers from the canopy of each of the five individuals were sampled. On the basis of the mean distance, species were recorded as low (<25 cm), medium (25–50 cm), and high (>50 cm).

Flower cover—The flower cover of species was estimated on the basis of a combination of their population size and number of flowers per individual during the flowering peak. Labiatae species were grouped into three categories, i.e., of low, medium, and large flower cover. These categories corresponded, respectively, to small-sized populations (<500 plant individuals), to large-sized ones (500–2,000 individuals), with few flowers on each individual (ten to 15), and to those dominating in the field during their flowering period; the latter concerned either large-sized populations (>500) with many flowers on each individual plant, or very large-sized populations (>2,000) with few flowers on each of them.

Essential oil production—This feature concerns the presence or absence of essential oil glands on corollas, observed under the microscope. Species were assigned accordingly as producing or nonproducing.

Flower life span—From May 1985 to May 1987, a minimum of 20 flowers for each taxon were followed on a daily basis from their opening to their wilting. The estimated flower life span was the mean of values recorded in different years.

Duration of anthesis—Observations were made in areas with the highest population density for each species. Sporadic occurrence of flowers was considered to be out of the flowering period of the species. Initiation, median date, and end of anthesis were recorded as calendar days (from 1 January).

Categories for each quantitative attribute were formed after statistical analysis using ANOVA and multiple Least Significance Difference (LSD) comparisons.

Nomenclature of plant species follows Flora Europaea (Tutin et al., 1972). Voucher specimens are deposited in the Herbarium of the Institute of Systematic Botany and Phytogeography of the University of Thessaloniki (TAU).

Pollinators—Pollinators were considered all animals, except for ants and spiders, that repeatedly visited flowers, fed on them, and made contact with any body part of any of the flower’s reproductive organs. This behavior was considered to result in pollination of a visited flower (Fager and van der Pijl, 1979). Each plant species was followed throughout its flowering period for at least 2 days out of every 20, and pollinators were recorded or captured. During these days, observations were made every 90 minutes from about sunrise until after sunset, each lasting for 30 minutes. Voucher specimens of the insect species are kept by the respective European specialists who made the identifications at the species level, whereas a part of the material is conserved in the collection of the senior author. The list of the insect species is given in the Appendix.

Statistical analysis—Because Labiatae share pollinators, we investigated the relationship between the pattern of floral attributes and the pattern of pollinator sharing. To this aim, a principal components analysis was run on two data sets concerning 1) the species attributes related to pollination, with characters having values from 0 to 4, depending on the attribute as defined above, e.g., 1–4 for corolla depth, 1–3 for corolla size, flower height, flower cover and nectar amount, 0–1 for essential oil production, and presence of each one of the five colors; and 2) all bee pollinators visiting more than one species of Labiatae. Only bees were considered in this analysis because they were reported and shown to be the predominant pollinators of the family and most numerous in phrygana. For each of the plant species, the recorded visit of any bee species was coded as 1 and absence as 0. Principal components analysis was made by use of the STATGRAPH-
TABLE 1. Pollination-related attributes of the ten Labiatae species in the Daphni phrygian ecosystem

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Life form</th>
<th>Life span</th>
<th>Color</th>
<th>Size</th>
<th>Depth</th>
<th>Height</th>
<th>Cover</th>
<th>Oil</th>
</tr>
</thead>
<tbody>
<tr>
<td>La</td>
<td>A</td>
<td>2.2 ± 0.11 (N = 25)</td>
<td>Purple</td>
<td>12.9 ± 0.35</td>
<td>14.6 ± 0.13</td>
<td>L</td>
<td>Me</td>
<td>No</td>
</tr>
<tr>
<td>Sv</td>
<td>B</td>
<td>2.3 ± 0.15 (N = 32)</td>
<td>Blue</td>
<td>9.8 ± 0.23</td>
<td>7.1 ± 0.18</td>
<td>M</td>
<td>Me</td>
<td>No</td>
</tr>
<tr>
<td>St</td>
<td>W</td>
<td>2.6 ± 0.19 (N = 25)</td>
<td>Pink</td>
<td>11.5 ± 0.26</td>
<td>11.9 ± 0.18</td>
<td>M</td>
<td>Lo</td>
<td>Yes</td>
</tr>
<tr>
<td>Pf</td>
<td>W</td>
<td>3.1 ± 0.24 (N = 26)</td>
<td>Yellow</td>
<td>21.1 ± 0.37</td>
<td>16.1 ± 0.21</td>
<td>H</td>
<td>La</td>
<td>No</td>
</tr>
<tr>
<td>Pm</td>
<td>W</td>
<td>2.8 ± 0.17 (N = 20)</td>
<td>White</td>
<td>10.0 ± 0.20</td>
<td>9.8 ± 0.22</td>
<td>M</td>
<td>Lo</td>
<td>No</td>
</tr>
<tr>
<td>Sh</td>
<td>W</td>
<td>2.4 ± 0.13 (N = 24)</td>
<td>Pink</td>
<td>7.0 ± 0.16</td>
<td>7.6 ± 0.16</td>
<td>M</td>
<td>Me</td>
<td>Yes</td>
</tr>
<tr>
<td>Sc</td>
<td>H</td>
<td>2.7 ± 0.20 (N = 26)</td>
<td>Pink</td>
<td>9.4 ± 0.17</td>
<td>7.4 ± 0.16</td>
<td>M</td>
<td>La</td>
<td>No</td>
</tr>
<tr>
<td>Tp</td>
<td>W</td>
<td>1.2 ± 0.08 (N = 30)</td>
<td>White</td>
<td>2.9 ± 0.12</td>
<td>4.2 ± 0.12</td>
<td>L</td>
<td>Me</td>
<td>Yes</td>
</tr>
<tr>
<td>Ba</td>
<td>H</td>
<td>1.4 ± 0.13 (N = 29)</td>
<td>Pink</td>
<td>9.7 ± 0.23</td>
<td>8.6 ± 0.17</td>
<td>M</td>
<td>Me</td>
<td>No</td>
</tr>
<tr>
<td>Tc</td>
<td>W</td>
<td>2.7 ± 0.14 (N = 37)</td>
<td>Pink</td>
<td>5.0 ± 0.14</td>
<td>5.4 ± 0.12</td>
<td>M</td>
<td>La</td>
<td>Yes</td>
</tr>
</tbody>
</table>

- *La = Lamium amplexicaule, Sv = Salvia verbenaca, St = S. triflora, Pf = Phlomis fruticosca, Pm = Prasium majus, Sh = Satureja thymbra, Sc = Stachys ceticca, Tp = Teucrium polium, Ba = Ballota acetabulosa, Tc = Thymus capitatus.
- A = annual, B = biennial, H = herbaceous perennial, W = woody perennial.
- Calendar day from 1 January.
- 4 d ± SE.
- 5 mm ± SE, N = 20.
- L = low, M = medium, H = high.
- Lo = low, Me = medium, La = large.

RESULTS

Plants—In the Daphni experimental site, Labiatae comprise 7.5% of all plant species displaying a biotic pollination syndrome (Petanidou, 1991b), which implies that pollinators are essential for their reproduction (Faegri and van der Pijl, 1979). The floral attributes for each of the ten species are given in Table 1. One and 2-day nectar production data correspond to the time of the day when nectar yield is high (Table 2).

Figure 1 shows the flowering phenology of the ten Labiatae species. Duration of anthesis is negatively correlated with time. The equation y = 89.408 - 0.351x (R = 0.792, P < 0.01), where y is the duration of anthesis and x the median date of flowering (calendar day, starting from 1 January), describes this relationship. No significant relationship was found between the median date of anthesis and the flower life span (P > 0.05). The ten Labiatae species can be separated into two groups. In the first, characterized by late winter-early spring flowering, belong Lamium amplexicaule, Salvia verbenaca, S. triflora, Phlomis fruticosca, and Prasium majus (early flowering group). The remainder belong to the group of late spring-summer flowering species (late flowering group). The two groups differ in their mean duration of anthesis (t-test, P < 0.05); 55.2 ± 3.0 (±SE) days for the early flowering and 36.0 ± 6.7 (±SE) for the late flowering.

Pollinators—All Labiatae species in phrygana were found to be insect-pollinated. In all, 201 insect species

TABLE 2. Nectar production of the Labiatae species in the Daphni phrygian ecosystem

<table>
<thead>
<tr>
<th>Dates of sampling</th>
<th>Time</th>
<th>Plant species</th>
<th>No. of flowers</th>
<th>Per flower nectar (µl ± SE)</th>
<th>No. of days</th>
</tr>
</thead>
<tbody>
<tr>
<td>30–31 March 1986</td>
<td>1400–1600</td>
<td>Lamium amplexicaule</td>
<td>32</td>
<td>0.63 ± 0.04</td>
<td>1</td>
</tr>
<tr>
<td>30–31 March 1986</td>
<td>1400–1600</td>
<td>Lamium amplexicaule</td>
<td>19</td>
<td>1.33 ± 0.05</td>
<td>2</td>
</tr>
<tr>
<td>27–30 March 1986</td>
<td>1100–1600</td>
<td>Salvia verbenaca</td>
<td>30</td>
<td>0.63 ± 0.05</td>
<td>1</td>
</tr>
<tr>
<td>27–30 March 1986</td>
<td>1100–1600</td>
<td>Salvia verbenaca</td>
<td>22</td>
<td>1.53 ± 0.10</td>
<td>2</td>
</tr>
<tr>
<td>31 March 1986</td>
<td>1300</td>
<td>Salvia triloba</td>
<td>4</td>
<td>2.55 ± 0.51</td>
<td>1</td>
</tr>
<tr>
<td>31 March–3 May 1986</td>
<td>1300</td>
<td>Phlomis fruticosca</td>
<td>34</td>
<td>1.47 ± 0.12</td>
<td>1</td>
</tr>
<tr>
<td>27 March–3 May 1986</td>
<td>1300–1600</td>
<td>Prasium majus</td>
<td>77</td>
<td>4.42 ± 0.21</td>
<td>1</td>
</tr>
<tr>
<td>6–7 May 1986</td>
<td>1100–1200</td>
<td>Stachys ceticca</td>
<td>8</td>
<td>0.44 ± 0.17</td>
<td>1</td>
</tr>
<tr>
<td>6–7 May 1986</td>
<td>1100–1200</td>
<td>Stachys ceticca</td>
<td>27</td>
<td>1.94 ± 0.18</td>
<td>2</td>
</tr>
<tr>
<td>2–4 May 1986</td>
<td>1200–1400</td>
<td>Satureja thymbra</td>
<td>33</td>
<td>0.48 ± 0.05</td>
<td>2</td>
</tr>
<tr>
<td>7–8 June 1986</td>
<td>1200–1500</td>
<td>Thymus capitatus</td>
<td>105</td>
<td>0.07</td>
<td>2</td>
</tr>
<tr>
<td>7–8 June 1986</td>
<td>1200–1500</td>
<td>Teucrium polium</td>
<td>25</td>
<td>Traces</td>
<td>2</td>
</tr>
<tr>
<td>8–10 June 1986</td>
<td>1100–1300</td>
<td>Ballota acetabulosa</td>
<td>55</td>
<td>1.92 ± 0.15</td>
<td>2</td>
</tr>
</tbody>
</table>
were observed making visitations (Appendix). They comprised 30.2% of the whole pollinating fauna of phrygana at Daphni (Petanidou, 1991a, b). Hymenoptera, and secondarily Diptera, comprise the most numerous orders of Labiatae pollinators. Solitary bees constitute 47.3% of all pollinator species. The early flowering group was visited by a total of 48 insect species, whereas the late flowering group was visited by 172 species. The number of pollinators per plant species is significantly higher in the late flowering group (t-test, $P < 0.001$; *Thymus capitatus* was excluded from the analysis because it supported an extremely high number of pollinators (123) compared with the other species).

Figure 2 shows the fluctuations of the number of Labiatae pollinators on a 10-day basis. Wasps first appear in the field in April (Petanidou, 1991b) but start visiting Labiatae flowers only in mid-May; they are most numerous during summer. *Thymus capitatus* and *Teucrium polium* flower late in the season and attract the majority of the wasp fauna available (61%). The pollinating fauna of *T. polium* consists mainly of wasps (nine vs. six bee species), in contrast to other Labiatae species (Appendix).

High numbers of bees are also recorded during late spring and summer. The distribution over time of the most important bee families, i.e., Anthophoridae, Megachilidae, and Halictidae, is shown in Fig. 3. Anthophorids are active mainly early in the season and are replaced subsequently by megachilids. The number of Halictidae remains relatively constant from mid-April to the end of the flowering season.

With the exception of *Apis mellifera*, bees generally have a short period of activity. There is no significant difference (t-test, $P > 0.05$) in the mean duration of activity of bees (*A. mellifera* excluded) visiting the early (69.9 ± 10.0 [±SE] days, $N = 35$) and the late flowering species (73.8 ± 6.5 [±SE] days, $N = 74$).

**Plant-pollinator relationships**—A total of 324 pollination events was recorded from all tropy levels. Tropy assignment for each pollinator was done on the basis of preexisting information concerning the plant-pollinator web of the whole phrygana community (Petanidou, 1991b). Thirty-seven species were monotropous, 15 of which were bees that belonged to Megachilidae (nine), Anthophoridae (four), and Halictidae (two). Six other nonmonotropous pollinators visited only Labiatae. Thus, 43 species, comprising one-fifth of the total pollinating fauna of Labiatae, are exclusively supported by this family. *Thymus capitatus* supports an exceptionally high number of pollinators (123) and 50% of the monocotropes of the family.

To detect whether there are associations of the major bee families with particular plant species or floral traits (i.e., color, size, depth, essential oil production, nectar amount), chi-square tests were run for each pairwise case (162 combinations). The combinations that shared significance were as follows: Anthophoridae and Megachilidae are associated with pink flowers ($\chi^2 = 5.374$, $P < 0.05$; $\chi^2 = 8.431$, $P < 0.01$, respectively) of small ($\chi^2 = 21.471$, $P < 0.01$; $\chi^2 = 7.343$, $P < 0.01$) or medium size corollas ($\chi^2 = 18.876$, $P < 0.01$; $\chi^2 = 7.629$, $P < 0.01$); Anthophoridae are associated with deep and very deep flowers ($\chi^2 = 10.233$, $P < 0.01$; $\chi^2 = 11.374$, $P < 0.01$); Halictidae and Colletidae are associated with small nectar...
The results of the principal component analysis are shown in Figs. 4 and 5. The late flowering species, located close to each other in Fig. 4 (based on floral traits), are scattered in Fig. 5 (based on shared bee pollinators). The opposite occurs in early flowering species in both analyses. This suggests that the high degree of floral resemblance among late flowering species did not result in a significant level of bee pollinator sharing, even though monotropical bees were not included in the analysis.

Corolla size, depth, and nectar production, related to flower presentation and reward, have high scores in the first component axis (Fig. 4). All three traits covary and show high values in the early flowering species. Thus, this intensifies their attractiveness to pollinators.

Regressions were run 1) between the first component scores of the floral attributes and those of the shared bee pollinators, 2) between the first component scores of the species attributes and the median date of the species anthesis, and 3) between the first component scores of shared bee pollinators and the median date of anthesis. Regressions for all three analyses were significant (Table 3). Consequently, the first component axis of both Figs. 4 and 5 can be interpreted as corresponding to the median date of anthesis and, therefore, also corresponding to time.

**DISCUSSION**

Summer drought is the prominent characteristic of Mediterranean climate (Aschmann, 1973). This limitation has an overriding influence on the evolution not only of the forms but also of the seasonal behavior pattern of organisms (Mooney and Kummerow, 1981). Phenological events, although related to a variety of other resources, are primarily linked to water availability. Flowering in Mediterranean ecosystems occurs mainly in the spring from March to June (Zohary, 1962; Shmida and Dafni, 1989; Petanidou, 1991b). In particular, the flowering period of Labiatae in phrygana extends from February to July and is related to the life form of the species. Woody species that are able to tolerate the harsh Mediterranean summer bloom in summertime (Fig. 1). The relatively late blooming is advantageous for these plants, because they may benefit from the abundant pollinators and avoid competition for pollination, which is more prominent early in the season. On the contrary, the only nonperennial species of Labiatae present in the system, i.e., *Lamium amplexicaule* (annual) and *Salvia verbenaca* (biennial), are the earliest to bloom in the season, whereas in herbaceous perennials blooming is staggered in between. Such a distribution of blooming times implies that flowering

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**Table 3. Results of the regression analyses**

<table>
<thead>
<tr>
<th>Parameters tested</th>
<th>R</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median date of species anthesis vs. first component scores of attributes</td>
<td>-0.723</td>
<td>0.0181</td>
</tr>
<tr>
<td>Median date of species anthesis vs. first component scores of shared bee pollinators</td>
<td>-0.844</td>
<td>0.0021</td>
</tr>
<tr>
<td>First component scores of attributes vs. first component scores of shared bee pollinators</td>
<td>-0.683</td>
<td>0.0295</td>
</tr>
</tbody>
</table>
of these species is related to their ability to tolerate intense water stress.

Another floral attribute related to climatic limitations is the reward obtained by pollinators. Due to these limitations, pollen plays a major role as a reward in phryganic ecosystems (Petanidou and Vokou, 1990), because nectar production is relatively low (Herrera, 1985; Petanidou, 1991b). In Labiatae, however, pollen quantity is limited and nectar becomes the principal reward. Moreover, Labiatae are among the most consistent nectar producers in Mediterranean ecosystems (Herrera, 1985; Petanidou, 1991b) and, consequently, offer the main water supply available to bees. Nevertheless, there is a difference in per-flower nectar production between the early and late flowering species (Table 2; Fig. 5). Per-flower nectar production of early flowering species was found to be significantly higher and may be related to water availability. Results by Dafni (1991) and Shmida and Dukas (1990) are similar. The excess in nectar production early in the season is accompanied by increased floral attractiveness (large and deep corollas), also noted by Dafni (1991).

The most important pollinator group of Labiatae is solitary bees. They consist of 95 species, 15 of which are specialists. In our phryganic ecosystem, the families of Compositae and Labiatae are important in hosting specialist bees (Petanidou, 1991b). Labiatae support mainly specialists restricted at the extremes of the flowering season. A prerequisite for bee specialization on Labiatae, however, is that besides nectar they can supply bees with the pollen needed as a nutritive source. Westrich (1989–1990) found that some solitary bees feed exclusively on Labiatae pollen.

The total number of Labiatae pollinators and the number of pollinators per plant species is higher in the late flowering group. This is in concordance with the general structure of the pollinator community in phrygana where pollinators are few early in the blooming season, but relatively numerous after April (Petanidou, 1991b). This suggests that the species of Labiatae flowering early in the season are more likely to face strong competition for pollination compared to the late flowering ones. Mosquin’s (1971) definition about cornucopian species does not hold in the case of Labiatae in phrygana, because species offering copious floral rewards, as observed in early flowering species, are not those abundantly serviced by pollinators.

The results of the principal component analysis and interpretation of the first axis of Figs. 4 and 5 suggest that the changes observed both of shared bee pollinators and of floral traits are related to time and, hence, to environmental gradients associated with its course (Table 3). There is a notable difference of the pollinator composition between early and late flowering species that is linked to a major shift of the pollinating fauna of the whole phrygian community occurring near the end of April (Petanidou, 1991b). Only 19 species (13 bees) of 201 pollinator species of Labiatae (98 bees) are shared by both early and late flowering groups. Considering the pollination-related floral traits of Labiatae (Figs. 1, 4), we can infer that the early flowering species are characterized by dissimilar, attractive, highly rewarding flowers with extended anthesis. These features could have resulted from competition for pollination that occurs mainly early in the season when pollinators are relatively few (Petanidou, 1991b). By contrast, in late flowering species, floral character differences are small and flowers are similar with regard to energetic floral allurement. The low investment to floral appeal in summer, both morphological and energetic, coincides with abundant pollinators. Moreover, it might be the result of a compromise between satisfying reproductive requirements and survival during the harsh Mediterranean summer under the limited energetic budget of stored reserves. This limitation is due to the fact that primary productivity in phrygana is negative from May to September (Margaris, 1976), which means that woody plants have to draw from reserves accumulated during the favorable-to-growth period (October to April) in order to cover their energetic requirements at that time.

Shift of flowering times and floral character displacement of co-flowering species have been demonstrated by numerous authors (see Waser, 1983; Motten, 1986 and literature cited therein) as mechanisms through which plant species partition the visitor resource. In the case of phryganic Labiatae, the divergence of flowering times throughout the flowering season, and of floral characters early in the season, may have resulted from competition for pollinators because the majority of Labiatae pollinators are generalists. Generalists, rather than specialists, are more likely to act as selective agents promoting floral character/reward differentiation and/or shift of flowering times (Heinrich, 1983; Waser, 1983 and literature cited therein). Most of the Labiatae pollinators also visited other members of the plant community under study. Petanidou (1991b) found that the honeybee visits another 95 phryganic species other than Labiatae in the same community. Therefore, competition for pollinators is expected to occur not only among Labiatae taxa, but also between them and other co-flowering species of the phryganic community. This holds particularly for the early flowering group, when pollinators are relatively few and the number of plant species in flower is comparatively high (Petanidou, 1991b). Differentiation of floral traits early in the flowering period might be driven by selection for pollinator constancy through floral gestalt rather than merely reward. By contrast, the late flowering Labiatae are in anthesis at a time when such changes are not at a premium given the abundance of the pollinator resource.

There has been selection for divergence of flowering times resulting in the formation of two species groups in Labiatae of phrygana. These groups represent two different pollination profiles with duration of anthesis, reward to pollinators, floral attractiveness, and floral character differentiation being the discriminant elements. All of these factors maximize early in the flowering period, thus optimizing the species competitive ability at a time when pollinators are not abundant. Whether this is a unique characteristic of Labiatae or rather a general trend in the phryganic ecosystem needs to be explored further.

LITERATURE CITED

**APPENDIX. Continued**

Coleoptera (22)


Lepidoptera (18)


Heteroptera (3)

Miridae (1): *Psalis ancorifer ancorifer* (Fieber) [Sc, Tp]. Pentatomidae (2): *Dolycoris baccarum* (Linnaeus) [La], *Odontotarsus* sp. [Tc].

Neuroptera (1)

Nemopteridae (1): *Nemoptera* sp. [Tc].

*septendentatum* (Laireille) [Ba, Pf, Pm, Sc, Sh, Sv, Tc, Tp], *Stelis punctulatissima* (Kirby) [Tc].

**Hymenoptera non Apoidea (26)**

Braconidae (1): *Braconidae* sp. indet. [Tc]. Chrysididae (1): *Chrysis analis* Spinola [Tc]. Eumenidae (5): *Chlorodynerus ypsilon rhodius* (Bluethgen) [Tc]. *Eumenes dubius* Saussure [Tc, Tp], *E. lunulatus* Fabricius [Tc], *Leptochilus alpestris* (Saussure) [Sh], *Parapodynerus euphiophilus* (Klug) [Tc, Tp]. Gasteruptiidae (3): *Gasteruption granulitator* (Tournier) [Tc]. *G. rubricans* Guerin [Tc, Tp], *G. terrestris* Tournier [Tc]. Masaridae (1): *Cerelis abbreviata* Villeneuve [Sh, Tc], Scelidae (3): *Scolia galbula* (Pallas) [Tc, Tp], *S. hirta* Schrank [Ba, Tc], *Tripis quinquemaculata* (Fabricius) [Tc, Tp]. Sphecidae (10): *Ammophila heydenii* Dahlbom [Tc], *Bembix pallida* Radoszkowski [Tc]. *Cerceris flavicornis* Brunel [Tc]. *C. sabulosa* Panzer [Tc], *Sceliphron destillatorium* (Illiger) [Tc], *Sphex pruinosus* Germar [Tc]. *S. rufocinctus* (Brunel) [Tc], *Stizoides tridentatus* (Fabricius) [Tc]. *Stizus ruficornis* (Fabricius) [Tc, Tp]. *Tachysphex incertus* (Radoszkowski) [Tc, Tp]. Vespidae (2): *Polistes dominulus* (Christ) [Tc], *P. gallicus* (Linnaeus) [Tc].

Diptera (33)


APPENDIX. Continued