Chapter 8

ECOLOGICAL AND EVOLUTIONARY ASPECTS OF FLORAL NECTARS IN MEDITERRANEAN HABITATS

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1 NECTAR SECRETION IN MEDITERRANEAN HABITATS

Owing to its superb sweet taste, nectar has, since antiquity, been considered the drink of the gods, which underlines its importance as a major daily allurement for insects to visit flowers. This is because nectar is the major source of energy to pollinators, providing them with sugars, other nutritious substances such as amino acids, and possibly minerals. Furthermore, nectar generally constitutes the only form of water intake for such pollinators.

Unlike pollen, the other prime reward for pollinators, nectar functions solely as a reward and secretion can continue after its removal (Proctor et al., 1996). Even if the magnitude of its importance has been questioned for some areas like the Mediterranean (Herrera, 1985; Petanidou & Vokou, 1990; Petanidou & Lamborn, 2005), nectar still constitutes an irreplaceable and unique attractant for pollinators within flowering plant communities (Proctor et al., 1996), and as such is likely to be subject to selection pressures imposed by pollinators (Petanidou, 2005; Petanidou et al., 2006). Consequently, nectar may differ greatly among phylogenetically related plants pollinated by different animals (Pyke & Waser, 1981; Baker & Baker, 1982), even though genetic (Percival, 1961; Baker & Baker, 1983) and ecological constraints (Corbet, 1990; Petanidou & Smets, 1996; Petanidou et al., 1999, 2000;

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Petanidou, 2005) may serve to limit the role of selection in shaping nectar characteristics.

The main nectar characteristics are volume, concentration, and sugar content, odour, colour, and taste, which may relate to the concentration and composition of dissolved sugar and non-sugar solids, such as amino acids, minerals, or phenolics (Thorp et al., 1975; Baker & Baker, 1983; Olesen et al., 1998; Adler, 2000a; Raguso, 2004; Petanidou, 2005; Petanidou et al., 2006). Of all nectar traits, the one that has received the most attention is quantity (volume, also in combination with sugar concentration), probably because of the ease of obtaining measurements (see Zimmerman, 1988 and Corbet, 2003 for reviews). In addition, many studies have focused on the qualitative aspect of nectars, with special attention given to the evolutionary and ecological significance of the two major components, sugars and amino acids (for reviews, see Petanidou, 2005; Petanidou et al., 2006; Nicolson & Thornburg 2007, Chapter 5 in this volume).

As nectar is an aqueous solution, its secretion depends largely on water availability. This implies that in areas with extreme water deficits, such as desert and other arid climate regions, plants may face major costs in secreting nectar. In the Mediterranean region, largely influenced by an extensive summer drought, plants are expected to face severe water stress when flowering towards the onset of, or during, the dry season. This drought regime may strongly affect secretion and other nectar attributes, and could select against nectar being produced as the sole reward (Herrera, 1985; Petanidou & Vokou, 1990). Scrutinizing previous literature, Petanidou and Lamborn (2005) discussed evidence for the importance of pollen versus nectar in Mediterranean pollination systems, which is supported by the low number of butterflies as exclusive nectar consumers (Petanidou & Ellis, 1993), the high abundance of typically low-nectar-producing species (Petanidou & Smets, 1995) and the high numbers of nectarless deceptive orchids (Dafni & Bernhardt, 1990; Dafni & O'Toole, 1994) found in this region.

In this chapter, I examine the factors that may shape nectar characteristics—such as quantity (volume) and quality (sugar and amino acid composition and concentration)—in Mediterranean habitats. These factors may be ecological (abiotic and biotic), phylogenetic, or co-evolutionary, with different pollinator guilds imposing selection. I address (i) the relative importance of the above factors in shaping nectar secretion, (ii) whether nectar is important in enhancing pollinator/bee diversity in Mediterranean communities, and (iii) whether Mediterranean communities differ from other plant communities in nectar composition. I conclude by focusing on the importance of Mediterranean areas for bee conservation, with results drawn from this study, as well as considering the potential impact of human management on these communities, particularly the major managerial issues of invasive species, beekeeping, and bumblebee-assisted crop pollination in greenhouses.

Most of the data presented in this review are drawn from studies carried out in Mediterranean habitats, especially East Mediterranean scrub, and in particular from a 30 ha *phrygana* community at Daphni, 10 km west of the city of Athens, Greece (see Petanidou & Ellis, 1993, 1996 for site description). Most of the data used have been published elsewhere, although some new conclusions are proposed based on unpublished data sets.

2 CHARACTERISTICS OF MEDITERRANEAN NECTARS

2.1 Nectar constituents of Mediterranean nectars

In general, floral nectars are mixtures of natural products consisting primarily of carbohydrates (mono-, di-, and oligosaccharides) accompanied by a wide variety of minor components, such as amino acids, proteins, enzymes, lipids, phenolics, glycosides, salts, alkaloids, vitamins, and other organic acids, and minor compounds (Lüttge, 1977; Baker & Baker, 1982, 1983; Kearns & Inouye, 1993; Adler, 2000a; Dafni et al., 2005). Floral nectars in the Mediterranean do not differ from these norms in term of composition.

2.1.1 Sugars

Sucrose, glucose, and fructose are the “big three” sugars most commonly found in nectar (Percival, 1961; Baker & Baker, 1983; Dafni et al., 1988; see also Nicolson & Thornburg, 2007, Chapter 5 in this volume). Minor sugars, such as sorbitol, melibiose, maltose, and mannitol are usually also present (Baker & Baker, 1983). This also applies to Mediterranean nectars (Petanidou, 2005).

Based on HPLC analyses of the nectars of 73 plant species, found in *phrygana* at Daphni, sucrose was present at an average of 702.5 ± 234.2 nmoles/flower, glucose at 869.4 ± 415.9 nmoles/flower, and fructose at 905.9 ± 412.0 nmoles/flower (Petanidou, 2005). In addition to these three sugars, traces of minor sugars were also detected, such as sorbitol (9 species); melibiose (7 species); maltose and mannitol (4 species each); ribose, mannose, and stachyose (2 species each); and arabinose, lactose, and trehalose (1 species each) (Petanidou, 2005).

Considering only the three main sugars, this phryganic community can be divided into species with “high sucrose” floral nectars (sucrose-dominant to sucrose-rich, according to the terminology of Baker and Baker (1983), which uses the sucrose/hexose ratio as a discriminating value) and “low sucrose” (hexose-dominant to hexose-rich) nectars (Petanidou, 2005). This does not imply that sugar composition of nectar is constant throughout the flower lifespan. Petanidou et al. (1996) showed that in *Capparis spinosa,* flower aging had an irreversible effect on nectar quality, which was expressed as a continuous decrease of the nectar sucrose/hexose ratio (as a result of sucrose breakdown) while the glucose/fructose ratio remained practically constant (approximately 1). The authors also concluded that the rate of sucrose breakdown was regulated (slowed down) by high sugar concentration, which implies a high invertase activity in dilute nectars versus low activity in concentrated nectars (see also Pate et al., 1985). This is very important from the nectar conservation point of view in regions with high temperatures such as the Mediterranean.

Just over half the species in Mediterranean communities have high-sucrose nectars (53.5% of the species according to Petanidou, 2005). Furthermore, species with high-sucrose nectars have the propensity to flower in spring and summer (60.8% of the species flowering then have high-sucrose nectars), whereas high-hexose nectars occur in winter flowers (63.6%) (Petanidou, 2005). The selection of high-sucrose against high-hexose nectars can be partly explained as a result of the drought constraint in the Mediterranean area, because high-hexose nectars consume more water than nectars with high concentrations of sucrose for the same amount (weight) of sugars contained, i.e., for the same sugar content (see discussion under “Water stress” on page 355; cf. Nicolson, 1998, 2002). It is unknown whether this is a specific characteristic of the Mediterranean region as no comparable data are available for other world communities.

2.1.2 Amino acids

Several amino acids have been found in floral nectars, all in much lower quantities than sugars (Baker & Baker, 1978, 1982, 1986; Gottsberger et al., 1984; Gardener & Gillman, 2001b; Chapter 5 in this volume). In the phryganic nectars, 22 amino acid compounds or groups of compounds have been detected (Petanidou et al., 1996, 2006). Cysteine and proline (including hydroxyproline) were not detected in phryganic nectars, owing to the analytical methods

Table 1. Amino acids detected in the floral nectars of *phrygana* using HPLC analysis. Values for particular amino acids, calculated from the data given in Petanidou et al. (2006), are averages over all plant species in the community (*n* = 73, excluding *Thymelaea hirsuta* and *Crocus cancellatus* with possible nectar contamination by pollen). Three different amino acid compounds are lumped together under "unknown". "Total amino acids" is the sum of all amino acids in the nectar. Amino acids that were not commonly detected in the nectars are flagged with * (found in less than 70% of the study species) and ** (in less than 10% of the species).

Amino acids	**Mean quantity (pmoles/flower)**	**SE**	**% of total amino acids**
Arginine	78	17.4	2.8
Asparagine	152	43.8	5.6
Aspartic acid	234	140.0	8.6
Glutamic acid	66	16.7	2.4
Glycine + threonine	218	35.3	8.0
Histidine + glutamine	231	61.6	8.5
Isoleucine	33	6.6	1.2
Leucine	52	10.1	1.9
Lysine	68	11.9	2.5
Methionine*	55	23.8	2.0
Ornithine	101	17.5	3.7
Phenylalanine	715	229.5	26.2
Serine	166	26.2	6.1
Tryptophan	43	11.2	1.6
Tyrosine + alanine	250	40.2	9.2
Unknown*	71	21.5	2.6
Valine	119	18.7	4.4
H-serine**	2	2.1	0.1
β-Alanine**	3	1.9	0.1
GABA (γ-aminobutyric acid)*	75	24.6	2.7
Total amino acids	*2,731*	*469.1*	*100.0*

used by the authors. (These amino acids are relatively common in some of the nectars originating from areas outside the Mediterranean: Baker & Baker, 1978; Gottsberger et al., 1984; Gardener & Gillman, 2001b). The same holds for taurine and AABA (i.e., α-aminobutyric acid), both found in the English nectars analysed by Gardener and Gillman (2001b). Of all the amino acids detected in the nectars of *phrygana*, 15 were common to nearly all nectars of the 73 species tested (Table 1, Petanidou et al., 2006). The authors compared their data set to those given by Gardener and Gillman

(2001b) and found that in general, amino acid concentration appears to be much higher in *phrygana* than in temperate systems (Petanidou et al., 2006).

Among all amino acids detected in the nectars of *phrygana*, the most prevalent was phenylalanine, both in absolute content and in concentration (Petanidou et al., 2006). Within all plant taxonomic groups, the most phenylalanine-rich nectar was that of Lamiaceae, with an average phenylalanine content of 47.2% of the total amino acids detected in all the species nectars of the family. Almost all phenylalanine-rich plants were keystone species of *phrygana* including *Stachys cretica*, *Phlomis fruticosa*, *Satureja thymbra*, *Urginea maritima*, *Asphodelus aestivus*, and *Thapsia garganica*. In a similar study carried out in an Israeli *batha* (i.e., a habitat that is equivalent to the Greek *phrygana*) Dafni et al. (1988) also found extremely high proportions of phenylalanine in the nectar of *Satureja thymbra* and *Salvia fruticosa* (71% and 52%, respectively). The high proportion of phenylalanine therefore seems to be characteristic of the phryganic plants in the Mediterranean region, as this amino acid was not detected at high levels in the nectars of other species from temperate and tropical systems (Baker & Baker, 1978, 1982, 1986; Gardener & Gillman, 2001b).

Until the early commencement of flower senescence, most if not all of the amino acids in nectar originate from phloem sap (Fahn, 1988). After the beginning of senescence, amino acids increasingly result from nectary breakdown (Petanidou et al., 1996). This type of proteolytic breakdown may be limited by sugar concentration, as found in the nectar of the Mediterranean species *Capparis spinosa* (Eisikowitch et al., 1986; Petanidou et al., 1996), which implies that sometimes nectaries may restrict amino acid flow through the nectar.

2.1.3 Minerals in floral nectars

Nectars have been found to contain K, P, Mg, Na, S, Ca, and many other minerals, with potassium prevailing in most cases (Waller et al., 1972; Kearns & Inouye, 1993; Liu et al., 2004; Dafni et al., 2005). No studies on mineral content have been performed specifically on nectars from the Mediterranean, but it is entirely probable that similar contents and concentrations are found in this region.

2.1.4 Secondary compounds

Apart from the main ingredients of sugars and amino acids, nectars often contain specific constituents or secondary compounds that may affect the attractiveness of nectar to pollinators and could therefore play a significant role in the pollination process. Phenolic compounds, for instance, may positively contribute to the taste of nectar at very low concentrations (Baker, 1977), while at other times—especially in higher quantities—they may repel honeybees (Adler, 2000a; Hagler & Buchmann, 1993).

In the Mediterranean, several secondary compounds have been identified in the nectars of plants associated mostly with honey-making. Such compounds include grayanotoxins (in the nectar of *Rhododendron luteum*; Buys, 2000), flavonoids (e.g., kaempferol, in the nectar of rosemary *Rosmarinus officinalis*; Ferreres et al., 1998), and glycosides (e.g., amygdalin, a cyanoglycoside found in the nectar of the almond *Amygdalus communis*; London-Shafir et al., 2003; and arbutin in the nectar of the strawberry tree *Arbutus unedo*; Pryce-Jones, 1944). The presence of such substances makes nectar either toxic (e.g., in *Rhododendron luteum* and *Amygdalus communis*) or at least repellent to some visitors. The evolutionary significance of such toxic nectars remains, to a major extent, unknown.

2.1.5 Nectar viscosity

Another characteristic of Mediterranean nectars that might be related to the presence of secondary compounds is viscosity. Nectar viscosity is mainly related to sugar concentration, which is high in the region (Kearns & Inouye, 1993; Petanidou & Smets, 1995). It may also result from rapid evaporation of the exposed nectars of many species—especially those with open flowers, e.g., *Urginea maritima*, *Thapsia garganica*, *Euphorbia acanthothamnos*, and *Ruta graveolens* (Dafni & Dukas, 1986; Petanidou & Smets, 1995). Yet, the viscosity of nectar may also be due to the presence of pectic substances as a result of post-secretory hydrolytic phenomena (Saeed et al., 1975); the presence of polysaccharides may also contribute to high nectar viscosity (Josens & Farina, 2001; Dafni et al., 2005).

An interesting case of nectar viscosity has been detected in the nectar of the *phrygana* species *Phlomis fruticosa* (Petanidou, 1991; Petanidou & Smets, 1995). Repeated observations over time showed that two types of flowers appeared in a patchy distribution on the same and over several individual plants: one with viscous and another with non-viscous nectar (Petanidou, unpublished data). Interestingly, these flower types did not differ in sugar concentration measured by HPLC analysis, but flowers with viscous nectars had a significantly higher sucrose/hexose ratio and higher total amino acid content (Table 2), implying that viscosity was caused by proteolytic phenomena resulting in an amino acid excess in these nectars. A more focused glance at the data showed that among all the amino acids and amino acid compounds detected, GABA was the only amino acid with an extremely high contribution in non-viscous versus viscous nectars (decreasing by 99% in the latter). Other amino acids (valine, phenylalanine, methionine, tryptophan, arginine, alanine + tyrosine) had much higher contributions in viscous versus non-viscous nectars, with valine showing the highest increase in viscous nectars (169%). Because GABA is an amino acid absolutely dependent on the presence of common salt (NaCl) (Keynan & Kanner, 1988; Wolfersberger, 2000), its higher content in non-viscous nectars may indicate that these nectars are additionally protected against an early breakdown by their higher NaCl content.

The evolutionary significance of viscosity as a nectar characteristic is as yet unknown, but it can be presumed that higher viscosity—if mostly due to protein hydrolysis—assists in the preservation of nectar attributes by contributing to the slowing down of disaccharide breakdown (cf. Table 2). In this way the large and long-lasting flowers of *Phlomis fruticosa* may preserve their high-sucrose nectar throughout anthesis while waiting for their relatively infrequent pollination partners, viz. long-tongued specialist bees (Petanidou, 1991; Petanidou et al., 1995). By limiting sucrose breakdown, higher viscosity favours water economy in the plant, as no excessive water is consumed to keep nectar concentrations stable in case of sucrose hydrolysis (Nicolson, 1998; Petanidou, 2005). The presence of two different types of nectar in the flowers of the same individual and within the same population of *Phlomis fruticosa*, i.e., a non-viscous type protected by the presence of GABA and NaCl, and a viscous type as a result of protein hydrolysis, highlights the importance of nectar preservation under the harsh Mediterranean conditions, an issue that undoubtedly needs further investigation.

2.2 Issues of nectar quantity and quality

In general, nectar secretion (quantity) at community level is lower in the Mediterranean compared to other regions. Cruden et al. (1983) found an average of 2.10 ± 0.67 μl nectar volume produced per flower of exclusively bee-visited species (n = 12) in the southwestern United States. In tropical systems, Opler (1983) distinguished between highly rewarding, large bee-pollinated species producing 9.75 ± 4.350 μl of nectar (n = 19), and low rewarding, small bee/wasp-pollinated species secreting only 0.63 ± 0.182 μl (n = 14) of nectar per flower. In contrast, per flower nectar yield in the Mediterranean is always low: in a Spanish *garrigue* community, Herrera (1985) could not ascertain the presence of nectar in 41% of the species studied (n = 122), concluding that in total only 35% of the species could be considered

Table 2. Different nectar attributes of viscous and non-viscous nectars of 1-day flowers of *Phlomis fruticosa* collected on 28–29 April 1992 in the phryganic habitat of Daphni, Athens. Values are averages ± SE followed by the results of statistical analyses (Mann-Whitney U tests).

Nectar attributes	**Viscous nectar**	**Non-viscous nectar**	**M-W U test**
Total content (nmole/flower)			
Amino acids	18.7 ± 1.75	5.22 ± 0.82	$U_{(8,16)} = 2$, $P < 0.001$
Sugars	6,880 ± 3,354.4	3,834 ± 2,504.2	$U_{(8,10)} = 20$, $P > 0.05$
Sucrose/hexose ratio			
S/(G+F) (in weight)	4.7 ± 0.72	3.3 ± 0.62	$U_{(8,10)} = 6$, $P < 0.01$
S/(G+F) (in moles)	2.5 ± 0.38	1.7 ± 0.32	$U_{(8,10)} = 6$, $P < 0.01$

nectariferous. In the Daphni *phrygana* community Petanidou (1991) found that only 12.4% of the species were nectarless (*n* = 133), but from the rest only 13.5% produced considerable quantities of nectar. In a more detailed study within the same *phrygana,* Petanidou and Smets (1995) and Petanidou (2005) found an average nectar secretion of 0.64 ± 0.246 µl per flower (*n* = 76 species). However, this substantial average was due to only a few abundantly nectar-secreting species. When three of the abundant nectar producers were removed, average secretion dropped by almost one third.

Nectar concentration (quality) in Mediterranean habitats is generally higher than in temperate communities (Beutler, 1930, 1953a, b; Cruden et al., 1983). Beutler (1930) found that the concentration of flower nectars of 18 species visited by honeybees ranged from 10–70%. von Frisch (1967) examined 65 species and found a similar range. The concentration found by Cruden et al. (1983) was 32.5 ± 2.46% (*n* = 12). On the other hand, Herrera (1985) found that in a Spanish *garrigue* most species had very concentrated nectars, usually higher than 60%. In the Greek *phrygana*, the community average concentration was 55.4 ± 1.69% w/w sucrose (*n* = 68). The species average concentration reached 76% w/w sucrose, while that of individual flowers could exceed 80% (Petanidou & Smets, 1995). In extreme cases (e.g., *Urginea maritima, Anthyllis hermanniae*), nectar may even crystallize in all flowers within a population and it cannot be sampled using capillaries (Petanidou, personal observations). Regardless of the small volumes detected in *phrygana*, the total amount of per flower nectar sugars is comparable to other temperate systems (Cruden, et al., 1983; Petanidou & Smets, 1995). The low nectar volume in *phrygana* coupled with a high energetic content is almost certainly related to water limitations in the Mediterranean area.

2.3 Plant species with no nectar

An important feature of Mediterranean plants is the absence of nectar from plants that one expects to be nectar-rewarding, based on their floral display. Such non-nectariferous species occurring in the Mediterranean region can be grouped into three major categories:

1. Species with nectarless deceit flowers, very commonly found in Orchidaceae in the region (Dafni & Bernhardt, 1990; Dafni & O'Toole, 1994). In deceptive pollination, pollinators are offered no floral reward, i.e., no nectar or pollen, for their visits to orchids (Dafni, 1984). Considering the high number of deceptive orchids in the Mediterranean area, it may be concluded that such a rewardless investment service may be of highly selective significance here. For instance, orchids comprise ~4% of the total angiosperm flora of the island of Lesvos, Greece, which may increase to 5% if all orchid subspecies are considered (Bazos, 2005, personal communication).

2. Species with differential investment in advertisement versus little or no reward. This group includes genera with showy flowers that have little or no nectar, and that use "discovery advertisement" sensu Dafni (1996), such as geophytes with autumnal flowering and hysteranthous foliage (e.g., *Colchicum, Cyclamen, Crocus*). It also includes plants with big and showy flowers blooming in spring, like *Acanthus spinosus* and *Bellardia trixago*, both with large white flowers (Petanidou, 1991). Although the rationale for the existence of such nectarless species would fit with that of deceptive pollination in the Mediterranean, the selection process towards flower emptiness is totally unknown for either species.

3. Species with differential investment in pollen versus nectar, both as advertisement and reward, which includes anemones (*Anemone*), poppies (*Papaver*, *Glaucium flavum*), and nightshades (*Solanum*). Such "pollen flowers" are common in the Eastern Mediterranean and very important to bees for pollen alone (Proctor et al., 1996). Other genera bearing less conspicuous and consequently less competitive pollen flowers (e.g., *Hypericum*), may be favoured by flowering during a less competitive period, i.e., towards summer, and then receiving pollinator services through necessity (Petanidou, 1999).

3 FACTORS SHAPING NECTAR SECRETION AND OTHER CHARACTERISTICS

The volume and concentration of nectar secreted by a flower depend on the following three factors: (i) ambient humidity and temperature (Corbet et al., 1979), (ii) selective reabsorption of solutes or water (Búrquez & Corbet, 1991; Nicolson, 1995), and possibly (iii) changes in the concentration at which nectar is secreted (Corbet, 2003). This means that nectar volume and concentration depend both on external conditions (climate, weather) and plant characteristics (e.g., related to structural and physiological attributes of plants and flowers). I discuss these factors in more detail below.

In a series of studies, Petanidou and Vokou (1990, 1993) and Petanidou and Smets (1995) argued that the severe water deficit and very high temperatures characterizing the Mediterranean summer and spring may have detrimental effects on nectar secretion rates and volumes (see also Herrera, 1985). As nectar secretion evidently continues even under extremely harsh conditions, one question is: to what extent are Mediterranean plants adapted to secrete nectar under unfavourable conditions, i.e., in high temperatures or low humidity?

3.1 Temperature

The nectar secretion rate increases with temperature, with an optimum dependent on the species in question (Fahn, 1949; Shuel, 1952; Beutler, 1953b; Huber, 1956; Corbet, 1990; Jakobsen & Kristjánsson, 1994). Petanidou and Smets (1996) hypothesized that because Mediterranean plants are adapted to high temperatures their optimal nectar secretion takes place at higher temperatures than that of temperate plants. In other words, relatively high temperatures could induce nectar secretion in Mediterranean plants. They tested their hypothesis on thyme *Thymus capitatus*, a typical *phrygana* plant, flowering under controlled temperature and humidity. Interestingly, nectar secretion in thyme flowers increased with temperature up to 38ºC as long as plants were not water-stressed or light-limited. The optimal temperature for nectar secretion was found to be 32.5ºC, much higher than optimal temperatures known for temperate species, e.g., *Oenothera biennis* (optimal temperature 24ºC), *Borago officinalis* (23.5ºC), and *Trifolium repens* (10ºC and 18ºC) (Shuel, 1952; Huber, 1956; Jakobsen & Kristjánsson, 1994). Petanidou and Smets (1996) also observed that in the open and under temperate summer conditions (i.e., low temperatures and solar irradiance) nectar secretion in thyme depended more on changes in light levels than on temperature. The authors concluded that temperature stress may stimulate nectar secretion in plants adapted to Mediterranean conditions. Such an adaptation may be most pronounced in summer-flowering species, which are visited by a large number of nectar-consuming insect species, as is the case with *Thymus capitatus* (Petanidou, 1991).

3.2 Humidity

A considerable part of the Mediterranean region is made up of coastal areas, where the sea has a dominant effect on terrestrial habitats. Pérez-Bañón (2000) found that in such habitats it is not primarily the temperature, but the differential humidity that positively affects nectar secretion, both in volume and sugar content. Working on *Medicago citrina*, a leguminous shrub in the archipelago of Columbretes, in Spain, the author discovered that the low relative humidity had a dramatic effect on nectar secretion. Nectar secretion was measured (i.e., volume, concentration, and sugar content per flower) on several mid-March mornings and ambient temperature and relative humidity were also recorded throughout the day. Amongst all parameters tested, the ones found to affect nectar secretion were (i) the mean of the maximal temperatures recorded over the 24 h preceding sampling, and (ii) the mean relative humidity recorded 2 h before sunrise (6:00–8:00). Further analysis of the data showed that mean relative humidity had a positive effect on both nectar volume and sugar content, which was more significant than that of temperature at all flower ages tested. The conclusion is that, in island communities, atmospheric humidity may play a very crucial role in nectar secretion that is otherwise limited by extreme water drought, evidently more important than temperature itself (Búrquez & Corbet, 1998).

3.3 Light intensity

Mediterranean plants are generally adapted to high light intensities and their nectar secretion is not expected to be limited by solar irradiance under normal Mediterranean conditions. Under unfavourable light conditions nectar secretion may decrease dramatically. Experimenting on *Thymus capitatus*, I found that, with a few exceptions, flowers in the sun secreted more nectar of a higher concentration than flowers growing mostly in the shade, implying limitation by solar irradiance (Petanidou, unpublished data). When *T. capitatus* plants were grown under typical temperate conditions (i.e., under low temperature and light intensity), solar irradiance was the most significant limiting factor for nectar secretion, not low temperature (Petanidou & Smets, 1996). The experiment was repeated with *Ballota acetabulosa*, another labiate species sympatric and co-flowering with *T. capitatus*, which differs in its microhabitat preference by usually growing in more shaded areas. *Ballota* appeared to perform optimally under temperate conditions where neither temperature nor solar irradiance appeared to limit nectar secretion (Petanidou & Smets, 1996).

3.4 Water stress

Because water is suspected to be a permanent limiting factor for nectar secretion in the Mediterranean, it is probably logical to assume that the highest nectar yields occur in the years of highest precipitation. Although there are no hard data, there is some support for this hypothesis from observations made in the wild on *Capparis spinosa*, *Thymus capitatus*, *Prasium majus*, *Satureja thymbra*, *Asphodelus aestivus*, and *Ornithogalum exscapum* (Petanidou & Smets, 1996; Petanidou et al., 1996; Petanidou, 1999).

To address the question of nectar secretion under water stress experimentally, Petanidou et al. (1999) studied the effect of irrigation on nectar secretion in three Lamiaceae species typical of *phrygana* (*Satureja thymbra, Stachys cretica,* and *Thymus capitatus*). Experimenting on potted plants taken from the wild, along with control measurements carried out on naturally growing non-irrigated potted plants, they found that after treatment only *T. capitatus* produced higher nectar volumes and total sugars per flower. Nectar yield in *S. thymbra* did not change with irrigation, whereas *S. cretica* showed dissimilar trends depending on the irrigation time within the flowering period. The authors concluded that irrigation may promote nectar secretion only in flowering periods that are unfavourable for growing, e.g., in summer. During such periods available water resources are probably allocated solely to nectar secretion—which may add up to considerable quantities—rather than to vegetative growth and excessive flower production, as may occur during spring.

Under typical Mediterranean conditions high-sucrose nectars predominate over high-hexose nectars, which implies that the former have been selected for (Petanidou, 2005). An explanation may be given by the overriding effect of drought, the most ecophysiologically effective constraint in the region. High-hexose nectars consume more water than high-sucrose nectars for the same amount (weight) of sugars (Nicolson, 1998, 2002). Therefore, by having high-sucrose nectars, Mediterranean plants avoid excessive water loss from hundreds of ephemeral flowers. In addition, by having high-sucrose nectars hidden within deep flowers, plants avoid nectar loss through evaporation during the hot and dry period of the year (Petanidou, 2005).

3.5 Nutrient stress

Lack of nutrients combined with water shortage may constitute another stress limitation to nectar secretion in Mediterranean plants. A first attempt to investigate the effect of nutrient application on nectar secretion was made by Shuel (1955) on non-Mediterranean plants. He concluded that nectar secretion is higher under low nitrogen supply. This conclusion was experimentally confirmed by Petanidou et al. (1999) in an extensive study carried out on Mediterranean plants. The authors investigated the effect of artificial nutrient supply on nectar secretion in three Lamiaceae species, both potted and naturally growing. Interestingly, they found similar results to those for irrigation (increased nectar secretion in the case of *Thymus capitatus*, no change in *Satureja thymbra*, and mixed trends in *Stachys cretica*). They concluded that irrigation is more important than nutrient supply in increasing per-flower nectar secretion, implying that the most influential external factor in shaping the physiology of nectar secretion in the Mediterranean is primarily drought, not nutrient scarcity. Owing to the production of surplus flowers on artificially fertilized plants (as a result of extended vegetative growth), a much higher number of nectarless flowers were found than on untreated plants (Petanidou et al., 1999). The presence of empty flowers has been considered to be of evolutionary significance, as it may enhance insect movements between flowers and plants, increasing visitation rates, reducing geitonogamy and thus increasing plant fitness (Brink & de Wet, 1980; Bell, 1986; Gilbert et al., 1991; Sakai, 1993). The results of Petanidou et al. (1999) indicate that this may apply particularly to regions experiencing long periods of drought, such as the Mediterranean.

Another effect of nutrient supply is the alteration of the chemical composition of nectar. Petanidou et al. (1999) found that nutrient application results in nectars having higher sucrose/hexose ratios than controls (although in *Thymus capitatus* the results were not significant). In the same series of experiments, amino acid concentration of nectars remained statistically unchanged after treatment with fertilizer. Treated flowers and controls, however, differed markedly in the relative abundance of certain amino acids, which were different among the three study species. In a similar study carried out in the UK, Gardener and Gillman (2001a) found that the concentration of total amino acids together with those of glutamine and proline increased significantly with increasing fertilizer treatment in *Agrostemma githago*, whereas the concentration of GABA decreased. Fertilizing also resulted in a significant decrease of the relative abundance of about half of the amino acids in the nectar of *Agrostemma*, with the exception of glutamine, which increased. The results of both studies show that the nectar complement can be influenced by soil conditions (cf. also Shuel, 1952, 1955; Shuel & Shivas, 1953), which may alter nectar attractiveness, and therefore have important implications at the plant–pollinator interface.

3.6 Ecological succession

Time is an important parameter in the framework of pollination ecology and several nectar secretion attributes appear to depend on flowering time, at least within a genetically related group of plants. Among all attributes Petanidou et al. (2000) studied in the Lamiaceae, only nectar concentration seemed to increase with flowering time, whereas the majority of attributes were affected negatively—flower depth and corolla width, the size of the nectary and its stomata, as well as the volume and sugar content of the nectar.

There is evidence that nectar secretion changes with time, not only in the course of the flowering season, but also within ecological time. A very interesting case is the change of nectar yield that some plants show in the course of post-fire succession in Mediterranean habitats (Petanidou & Ellis, 1996; Petanidou, 1999; Potts et al., 2003).

Firstly, this change may be a consequence of changes in the community structure, with annuals being gradually replaced by perennials as the system ages, combined with the fact that perennials bear more alluring flowers (i.e., more nectar-rewarding) than annuals (Petanidou & Smets, 1995; Petanidou, 1999). Potts et al. (2003) quantified some key parameters of both pollen and nectar forage at the community level in different ages of post-fire communities and showed that changes in floral reward structure reflected the general shift from annuals (generally low-reward open-access flowers) to perennials (mostly high-reward and restricted access flowers) as post-fire regeneration ensues. In particular, the authors found that nectar volume, water content, concentration, and the diversity of nectar-foraging niches are all greatest in the first post-fire stage of succession, i.e., immediately after fire, with a steady decrease as regeneration proceeds (Table 3). This is slightly different to what Petanidou and Ellis (1996) suggested—relatively low per-flower nectar quantity in the first post fire years. A similar decline with ecosystem age after fire was found in energy availability in nectar and pollen, and the relative importance of pollen to nectar energy (Potts et al., 2003).

Secondly, within the core of the main flowering season, perennials are much more competitive than annuals, the latter offering about half the nectar yield of the former (as per day sugar equivalent) (Petanidou & Smets, 1995; Petanidou & Ellis, 1996).

Thirdly, and most surprising, is the fact that some perennial plants may increase their nectar secretion during the mature phryganic stage whereas annuals/biennials may experience reduced secretion in the course of succession in Mediterranean communities (e.g., *Capparis spinosa*, *Phlomis fruticosa*, and *Stachys cretica* versus *Lamium amplexicaule* and *Salvia verbenaca*; Petanidou, 1999). Comparing the nectar standing crop of *Satureja thymbra* in burnt and unburnt areas in Israel, Potts et al. (2001) found similar results, with nectar standing crops two times higher in unburnt than in burnt habitats. As a result, in the course of ecosystem succession, perennials may become more attractive to bees and to other pollinating insects than annuals within the community, thus promoting their fitness through differential seed set. The conclusion drawn from all the above studies is that floral communities and associated rewards not only shape pollinator community structure, but also have significant implications for the process of succession.

4 MATCHING NECTARS AND FLOWER TYPES

High-volume nectars have generally been associated with deep and tubular flowers because of their smaller surface:volume ratio, which diminishes water loss through evaporation (Corbet et al., 1979; Plowright, 1987; Dafni, 1991). Freely exposed nectar in open flowers tends to equilibrate with ambient humidity (Corbet et al., 1979; Nicolson, 1998, 2002). Similarly, nectar concentration is more constant in deep flowers compared to open ones, which contain smaller volumes of nectar where concentration can fluctuate rapidly (Corbet, 2003).

These principles apply equally to the Mediterranean *phrygana*, where nectar volume is found to be positively correlated with flower depth ($R = 0.312$, $P < 0.01$), whereas nectar concentration shows a negative association ($R = -0.485$, $P < 0.000$) (Petanidou & Smets, 1995; Petanidou, 2005). Both floral depth and nectar volume are highly related to sucrose/hexose ratios in nectar at the community level ($R = 0.441$, $R = 0.426$, respectively; $P < 0.001$; Petanidou, 2005). One can conlude that the *phrygana* community is made up of two major sets of flower types and nectars (although intermediate values do exist): deep flowers with high, albeit dilute, volumes of sucrose-dominant to sucrose-rich nectars (such flowers may act as “nectar reservoirs” by slowing the rate of sucrose breakdown); and shallow or open flowers with less volume but more concentrated, hexose-rich nectars (Petanidou, 2005).

Among all the *phrygana* plant families, the Lamiaceae have the highest average nectar yield per flower and Asteraceae the lowest (Petanidou & Smets,

Table 3. Summary of the nectar attributes related to ecosystem post-fire succession. (Data are from Petanidou and Ellis (1996), Potts et al. (2003, 2004), Petanidou and Lamborn (2005)).

Attributes	**Freshly burnt site (1–2 year *phrygana*)**	**Intermediate age (15–25 year scrub)**	**Mature pine forest (>50 years)**
Nectar component			
*Volume**	low–medium–high	medium–low	medium
Per flower volume	relatively low	higher	higher
*Concentration**	medium–high	medium	medium–low
*Water content**	low–medium–high	medium–low	medium
Nectar niche diversity	high	lower	low
Energy reward*			
Pollen	high	medium	low
Nectar	medium–high	medium–high	medium
Pollen: nectar	high	medium	low
Plant component			
Plant diversity	high	medium	medium
Floral abundance	high	medium	medium
Plant groups	many annuals	fewer annuals	more perennials
Bee component			
Diversity	high	medium	low
Abundance	high	medium	low
Guilds	Mainly short-tongued bees; many Andrenidae and Apidae	Mixed guilds including long-tongued bees (Megachilidae); fewer Andrenidae and Apidae	Mixed guilds; many Andrenidae and Apidae

* per unit habitat area

1995). Dissimilar flower shapes, therefore, differ in their nectar volume, with gullet types secreting the highest and bowl- and head-shaped secreting the lowest volumes. Bowl-shaped flowers possess more concentrated nectars compared to gullet-shaped flowers (Petanidou & Smets, 1995).

Structural traits of flowers appear to play a major role in shaping nectar characteristics, at least within a phylogenetically related group of plants. This is true for flower size (i.e., corolla length and width) that is related to nectary size (cf. also Chapters 3 and 4 in this volume) and nectar yield (Dafni et al., 1988; Dafni, 1991; Petanidou et al., 2000; Galetto & Bernardello, 2004). The size of the nectaries and nectarostomata (i.e., the openings on the nectary through which the nectar is secreted) is positively correlated with nectar volume (Dafni et al., 1988; Petanidou et al., 2000). On the other hand, the number of nectarostomata does not appear to play a significant role in controlling nectar volume (Petanidou et al., 2000), which is in agreement with other continental (Teuber et al., 1980; Davis & Gunning, 1991), but not tropical species (Galetto, 1995; but see Galetto & Bernardello, 2004). Among all nectary attributes only the stomatal size affects nectar concentration and this is a negative relationship (Petanidou et al., 2000). Species with small nectarostomatal openings secrete more concentrated nectars, at least within the Lamiaceae (Petanidou et al., 2000). It is unknown whether this is a peculiarity of Mediterranean nectaries, or a general characteristic of all Lamiaceae, or even broader groups.

5 NECTAR AND THE POLLINATOR INTERFACE

5.1 Relating consumers to deep-flower nectars

Tubular, deep, and closed flowers can protect nectar from nectar thieves and unwanted insects, such as short-tongued visitors who will have limited access (Baker & Baker, 1983; Dafni, 1991; McCall & Primack, 1992; Menzel & Shmida, 1993; Potts et al., 2001). The presence of numerous hairs and stamens in the flowers of several Mediterranean species, such as those within the genera *Cistus* and *Capparis*, may have a role similar to long corollas in restricting air movement and excluding insects (Petanidou & Ellis, 1996; Petanidou, 2005). In this respect, the presence of honey leaves or honey pockets (i.e., petal scales where nectar is accumulated) in bowl-shaped flowers in some Mediterranean genera is probably related to a similar nectar-protective function (e.g., *Fritillaria, Nigella, Ranunculus*).

5.2 Nectar sugars and pollinators

High-sucrose nectars prevail in the Mediterranean, not only at the community level and during the major flowering season (spring), but also during the harshest season, i.e., summer (Petanidou, 2005). In addition to the reasons mentioned on page 346, the propensity of sucrose-rich nectar species to flower in spring–summer, versus hexose-rich species to flower in winter can be explained on the basis of:

- Co-evolution of plants with insects. By containing easy-to-digest monosaccharides (Nicolson, 1998), high-hexose nectars are more adapted to consumption by an extensive array of mainly non-specialized pollinators (e.g., short-tongued bees, wasps, beetles, butterflies, flies; cf. Petanidou, 1991). On the other hand, high-sucrose nectars are better adapted to more specialized pollinators such as long-tongued bees which are apt to perform sucrose digestion (hydrolysis). The dominance of hexose-rich nectars in winter coincides with the prevalence of non-specialized pollinator guilds (e.g., syrphid, anthomyiid, and other flies). Similarly, sucrose-rich nectars prevail in spring and summer together with their selective agents, the long-tongued bees. The presence of any high-hexose nectars during spring and summer is probably related to mixed guilds of insects that are active during that period (Petanidou, 2005).

- Trade-off between plant water economy and co-evolution with insect diet. For the same carbohydrate reward offered to pollinators, high-sucrose nectars utilize less water than high-hexose ones. Considering that calorific value is more important to bees (at least to honeybees; cf. Wells et al., 1992) than the type of sugars contained in the nectar (i.e., mono-, disaccharides), it could be concluded that in bee-dominated communities, such as those of the Mediterranean, selection favours high-sucrose over high-hexose.

5.3 Nectar amino acids and pollinators

Phenylalanine (present in 9.5% of the study species) and GABA (present in 63% of the species) were the only amino acids in the phryganic community that were consistently correlated with pollinator guilds and families (Petanidou et al., 2006). The effect was expressed as the relationship between the phenylalanine content of plant nectars (= % of total amino acid content) versus the number of species in pollinator guilds or families visiting them. Phenylalanine appeared to be positively related to long-tongued bees and megachilids. GABA could be correlated with to a broader array of insects—long-tongued bees, anthophorid and andrenid bees, as well as anthomyiid and syrphid flies.

On the other hand, several amino acids appeared to be sporadically repellent to a few insect groups. Asparagine appeared to repel many insect groups: beetles, bugs, anthomyiid flies, wasps, short-tongued bees and colletids, but only megachilids among the long-tongued bees). These characteristics seemed to be a result of co-evolution with bees—long-tongued bees, especially Megachilidae, seem to have played the major selective role for phenylalanine-rich nectars (Petanidou et al., 2006). This could be related to the fact that phenylalanine is an essential amino acid in bee diets (de Groot, 1953), an explanation that fits well with the classic ideas of Baker and Baker (1973a, b, 1978, 1986). Petanidou et al. (2006), however, go further by arguing that phenylalanine's most important effect for bees is its strong phagostimulatory quality, which is unique among many amino acids tested in other studies (Inouye & Waller, 1984). This quality certainly adds to the taste of nectar (Gardener & Gillman, 2002), hence influencing bee preferences and the plant–pollinator food web structure at the community level. Having such a potential, and owing to the high number of bee species in the Mediterranean, it is not surprising that phenylalanine dominates the nectars of plant species that are characterized by prevailing melittophily in this region, especially in the Lamiaceae (Dafni et al., 1988; Petanidou & Ellis, 1993, 1996; Petanidou & Vokou, 1993; Michener, 2000).

There are a few interesting species exceptions within the phenylalanine-rich family of Lamiaceae. The first is *Thymus capitatus* with a detected phenylalanine content at community average levels both in Israel and Greece (Dafni et al., 1988; Petanidou et al., 2006). A possible explanation is that *T. capitatus* constitutes a "pollinator sink" within both communities, visited by mixed insect guilds (123 insect species in the Greek *phrygana* of which bees comprise only 24%; Petanidou, 1991; Petanidou & Potts, 2006). It might be that plants flowering outside the main blooming season under conditions of little or no competition for pollinators, i.e., during the Mediterranean summer or early spring (Petanidou, 1991, 2004), are less challenged to produce extra phagostimulants, therefore have low levels of phenylalanine in their nectars (e.g., *Lamium amplexicaule* in Athens and *Rosmarinus officinalis* in Israel, as well as *T. capitatus* in both countries) (Dafni et al., 1988; Petanidou et al., 2006). The exception of *L. amplexicaule* could also be explained by the partly cleistogamous character of its flowers (Lord, 1982).

The case of GABA that is related positively with some insect guilds visiting the phryganic plants may be similar to that of phenylalanine. Petanidou et al. (2006) argue that phagostimulation may be related to the probable copresence of NaCl, a salt on which GABA strongly depends (Keynan & Kanner, 1988; Wolfersberger, 2000). There is some evidence that NaCl has a positive effect in attracting honeybees probably by improving nectar taste (Taber, 1991; Fulton, 1997; Gardener & Gillman, 2002). Perhaps in an area like the Mediterranean where sweetness can be of limited discriminatory value (all nectars are concentrated, see also next paragraph), it is the combination of GABA–NaCl that constitutes the most important nectar phagostimulant for several pollinating guilds (flies, bees, and beetles) that might have acted as selective agents for GABA-rich nectars.

In addition to the effect that particular amino acids may have in attracting pollinators to Mediterranean flowers, Petanidou et al. (2006) found that total amino acid content of nectar constitutes a very significant trait to which some pollinator guilds (anthophorids, megachilids, and apids) respond. This supports the general ideas of Baker and Baker (1982, 1986) that amino acids may have co-evolutionary significance in floral nectars. The novel finding by Petanidou et al. (2006), however, is that this positive effect is also applicable to solitary bees, as well as social honeybees and tropical stingless bees discussed by earlier studies (Roubik et al., 1995; Gardener & Gillman, 2002). The most important finding, however, is that total amino acid content of nectars versus sugar content is the most significant factor in shaping plant–pollinator interactions in the Mediterranean habitats. The explanation for this is probably related to the Mediterranean climate, as in such hot and dry habitats, characterized by very high sugar concentrations (Petanidou & Smets, 1995), the sweet taste of nectar may probably be too "strong" to function as species-specific discriminator and allurement. In these habitats, the high contribution of amino acid content, together with the presence of individual phagostimulants (e.g., phenylalanine, and possibly NaCl–combined GABA) may have been selected in addition and constitute the nectar traits that are specifically important in attracting particular insect guilds (Petanidou et al., 2006). It will be interesting to see if these trends are also found in other mediterranean regions and habitats, such as Chile, South Africa, and the Californian coastal scrub.

5.4 Nectar minerals and pollinators

Among all minerals present in floral nectars special attention was given to potassium, which was found to discourage honeybees from visiting onion flowers (Waller et al., 1972; Liu et al., 2004). Moreover, there is some evidence today that sodium (in the form of NaCl) has a positive effect on attracting honeybees (Taber, 1991; Fulton, 1997); NaCl may improve nectar taste significantly (Gardener & Gillman, 2002).

Plants contain a high K/Na ratio, which is reflected in the haemolymph of herbivorous insects, including the highly evolved bees, as a result of co-evolution with higher plants (Boné, 1944; Duchateau et al., 1953). This may also influence nectar–pollinator relationships (Hiebert & Calder, 1983). Given the deterrent character of potassium opposed to the attractive character of sodium (Waller et al., 1972; Liu et al., 2004), I hypothesize that, in general, highly attractive nectars are selected on the basis of their high Na/K ratio, especially those visited by highly evolved pollinators. Within *phrygana*, I expect that this will mostly apply to plant species visited by long-tongued bees, primarily Megachilidae and Anthophoridae. No doubt, future research on nectar attractiveness will explore these questions and hypotheses.

5.5 Nectar secondary compounds and pollinators

The presence of secondary compounds in floral nectars may enhance plant fitness both inside and outside the Mediterranean (see "Secondary compounds" on page 348). This may be achieved through different methods:

- Increasing pollinator visitation to plants defended against herbivore attack (Adler, 2000a, 2000b)
- Attracting more specialized pollinators (Masters, 1991)
- Influencing the preferences of foragers (e.g., phenol and alkaloid compounds; cf. Waller et al., 1972; Hagler & Buchmann, 1993)
- Increasing floral constancy of legitimate pollinators and inhibiting nectar thieves (Stephenson, 1981, 1982)
- Increasing interflower and interplant movements to avoid ingesting excessive levels of secondary compounds (London-Shafir et al., 2003).

5.6 Floral nectar, floral diversity, and bee diversity

Several studies have attempted to explain bee diversity using single quantitative nectar parameters at a community level, and it has been shown that changes in nectar levels influence bee visitation to flowers (see Proctor et al., 1996; Potts et al., 2003, 2004 for reviews). The most commonly used attributes have been spatial and temporal patterns of nectar volume and concentration. Although such parameters of nectar reward structure may define the suite of flower visiting, they fail to give a full picture of how the community is organized on the basis of these single aspects of nectar reward. In order to describe the nectar reward structure of Mediterranean communities, Potts et al. (2004) used a complex approach to quantify "nectar resource diversity" which they defined as the variety of nectar volume and concentration combinations available in a community. They found that the variation in bee species richness within a habitat is much better explained by such a parameter than by other nectar variables such as volume, concentration, energy value, and water content, which have little predictive value per se. In fact, the authors demonstrated that nectar resource diversity may be a fundamental factor organizing nectarivorous communities. Using a series of Mediterranean habitats differing in successional stage and structure, they found that nectar resource diversity is highly correlated with floral species richness and particularly with the species richness of annuals. In addition, nectar resource diversity is highly correlated with bee diversity, which illustrates the importance of this parameter in determining the flower–visitor web structure in Mediterranean communities. This is a key finding in view of the management of these communities, demonstrating the importance of mosaic structure combined in several successional stages in order to attain the maximal floral and bee diversity in a habitat (see also Petanidou & Ellis, 1996).

5.7 What types of nectars do pollinators prefer?

In the Mediterranean, as in many other regions and habitats, nectar profile (i.e., secretion and characteristics) is sometimes strongly related to the plant's main pollinator guilds (Baker & Baker, 1983; Petanidou, 2005; Petanidou et al., 2006). This may be reflected in differences in the nectar profile of genetically closely related plant species that are pollinated by different insect guilds. The pollination of several species and subspecies of *Capparis* in Israel is a case in point. The nectar of *C. ovata*, a hawkmoth-pollinated species, is higher in volume and concentration than that of *C. spinosa*, a bee-pollinated species, which occurs in the same localities and has a similar flower morphology (Dafni et al., 1987). In addition, the two subspecies of *C. spinosa* in Israel were found to have different nectar profiles: a hawkmoth-pollinated subspecies with high nectar yield and a bee-pollinated one with lower nectar volume and concentration (Eisikowitch et al., 1986).

Within the Mediterranean, however, cases like *Capparis* are not common, as this genus represents an exception for many reasons. Aided by a very efficient water economy, *Capparis* is a thriving genus in the Mediterranean region where it manifests diverse pollination systems and exceptional traits such as summer flowering and showy nocturnal flowers with unusually high nectar rewards (Rhizopoulou, 1990; Petanidou et al., 1996; Rhizopoulou et al., 1997). In fact, *Capparis* provides the most abundant nectar reward within Mediterranean scrub, with a recorded nectar volume of 15.21 µl per flower—about 24 times as much as the community average (0.64 µl) (Petanidou & Smets, 1995). On the other hand, a phryganic community encompasses an outstanding diversity of ordinary plant species that, unlike *Capparis*, follow the "system rules," by flowering mainly within the major blooming period (i.e., spring, from March to May) and having small, diurnal, and low-nectar-yielding flowers (Petanidou et al., 1995; Petanidou & Smets, 1995). Such habitats also contain an exceptional diversity of flower-visiting insects of particular taxonomic and ecological guilds (Petanidou & Ellis, 1993, 1996). This raises the question of whether, at the community level, there is a possibility of matching insect guilds and plant species on the basis of their nectar attributes. Petanidou et al. (2006) attempted to address this question in a community study and their results are summarized below:

1. Relationships with insects are more significant in distinguishing plant assemblages characterized by particular nectar traits than other plant

attributes, both taxonomic and ecological (flowering season, life form). This means that plant–pollinator co-evolution is probably more important in shaping nectar traits than ecological constraints or phylogenetic affinities.
2. In general, the discriminating nectar trait for the response of most insect guilds is amino acid composition, not sugar composition or nectar volume.
3. Bee response is mostly shaped by amino acid composition, whereas the response of other anthophilous insect guilds is mainly shaped by sugar composition.
4. Among all amino acids, asparagine and H-serine always have a negative effect on insect guilds, whereas phenylalanine has a positive effect (on long-tongued bees), as does GABA (on long-tongued bees and other anthophilous insect guilds).
5. Among major sugars, only fructose has a general positive influence on different insect guilds, especially on short-tongued bees and insects other than bees (hoverflies, anthomyiid flies, beetles, and wasps), while sucrose has a positive influence on long-tongued bees and glucose a negative influence on wasps.

In conclusion, even in a generalized system like *phrygana* (Petanidou & Potts, 2006), it appears that the nectar traits of plant species play an important role in organizing the community and its plant–pollinator resources. Perhaps we are at the beginning of unravelling the thread of the nectar secrets encompassing both gastronomy and the satisfaction of insects' physiological needs (Gardener & Gillman, 2002).

6 NECTAR AND MANAGEMENT OF MEDITERRANEAN HABITATS

6.1 Introduced and invasive plants: effects on wild flowers and bees

Invasive plants represent a major threat to world biodiversity and especially to the Mediterranean, one of the world hot spots for biodiversity (di Castri et al., 1990). Such plants often bear "more attractive" flowers, i.e., larger or more rewarding, which may bring about competition for pollination with the native flora, and may result in reduced seed set in native species (Memmott & Waser, 2002). The reduced seed set and biological fitness of the native species will have detrimental repercussions at the levels of both economics (e.g., reduced fruit or seed yield in agricultural systems) and nature conservation (e.g., local extinction of species).

Copiously offered nectar is often the most effective fee for an introduced alien species to establish and become invasive. Especially in the Mediterranean, where nectar is not abundant, efficient invasive plants are expected to be those offering high nectar or pollen yields. Such high nectar yields may also be available at the population level in situations of extremely high number of flowers that some plants or populations may have. This is the case for *Bunias orientalis*, an extremely successful invasive plant species in central Europe, which is a food source for bumblebees and honeybees, but has negative impacts on the fitness of native plant species (Schurkens & Chittka, 2001). Examples like this must raise the attention of managers and decision makers before any site management is implemented. In this respect, the deliberate introduction of the American species *Phacelia tanacetifolia* as a nectar source plant in central Europe and the Mediterranean is astounding, especially when considering the cost of irrigation in an area suffering from extreme drought (Petanidou, 2003).

6.2 Invasive bees: beekeeping, bumblebee management, and wild bee conservation

The diet of all bee species consists exclusively of pollen and nectar collected from flowers, although it may occasionally be supplemented by other substances, such as honeydew, plant sap, waxes, resins, and water (Michener, 1974). As a consequence, pollen and nectar are the most sought-after foods within a community, and the source of competition among bees and other flower-visiting insects, at least in periods when these resources are limited. Among all bees, honeybees and bumblebees are notorious for exploiting floral rewards, and a bulky literature has accumulated on their competitive efficiency against solitary bees (see Goulson, 2003, for a review).

Both honeybees and bumblebees possess undoubted foraging abilities. Apart from having relatively long tongues, these large and hairy animals thermoregulate in flight and retain heat within their large nests, therefore being able to exploit all sources of nectar in the community by foraging earlier in the morning than many native, solitary bee species or under unfavourable weather conditions, thus reducing the food base of other bees (Corbet et al., 1993; Dafni & Shmida, 1996; Willmer & Stone, 2004). In addition, they are generalists with large and long-lived colonies and so are able to adapt to a succession of different flower sources as they become available. Having such assets, it is no wonder that honeybees and bumblebees have proved to be highly competitive in various communities and most adaptable in colonizing new habitats far from the places of their origin. Considering that the colonized areas may be limited in nectar resources, these bees can constitute a threat to the local pollinator fauna, especially to small solitary bees in the cases where their foraging host breadths overlap. This applies particularly to the almost omnipresent *Apis mellifera*, which has been observed frequenting the majority of plant species within any one geographic region, visiting nearly 40,000 different plant species (Crane, 1990). The situation is also alarming within the Mediterranean, where honeybees are extensively managed for honey production not only in agricultural lands, but also in marginal lands, woodland and scrubland, as well as in protected areas. As an example, within the 30-ha *phrygana* community in Athens, *A. mellifera* was recorded visiting 103 out of the 133 available plant species (Petanidou & Potts, 2006). In such cases, honeybees could also be displacing native bees by just reducing their resource base (Petanidou & Ellis, 1996; Forup & Memmott, 2005).

Bumblebees (*Bombus* spp.), whose natural range is largely confined to the temperate northern hemisphere, have recently been introduced to various countries to enhance crop pollination. In the Mediterranean region, especially in typical Mediterranean habitats where bumblebees are relatively uncommon (Petanidou & Ellis, 1993), this fashion started in the 1980s and continues to date on an enormous scale, mainly in order to assist pollination in greenhouses. Following escapes from commercial colonies, such introductions lead to unwanted invasions, which may spread over large areas (Dafni & Shmida, 1996; Dafni, 1998).

It has been argued that depletion of nectar on a daily basis before native bees begin to forage, may result in a significant asymmetry in competition in favour of these introduced species (Goulson, 2003). On Mt Carmel in Israel, Dafni and Shmida (1996) reported declines in abundance of medium- and large-sized native bees (and also of honeybees) following the arrival of *Bombus terrestris* in 1978. Hingston and McQuillan (1999) recorded displacement of two species of *Chalicodoma* (Megachilidae) in Tasmania by introduced *B. terrestris*, which the authors consider a threat to Australian ecosystems (Hingston & McQuillan, 1998). Based on measurements of the high competitiveness of *B. terrestris* to native bees, it has been suggested that unregulated movements of non-native populations of the species within Europe should be banned without a full risk assessment (Ings et al., 2005). The impacts of *A. mellifera* introductions are similar: Goulson et al. (2002) found higher abundances of native bees in honeybee-free sites in Tasmania; Forup and Memmott (2005) observed some changes in floral host breadth of long-tongued bees as a result of colonization by honeybees, although they found no effect on short-tongued bees. In New Caledonia, unique systems of pollination mutualism have been endangered by the introduction of honeybees (Kato & Kawakita, 2004).

Mediterranean habitats are known for their high solitary bee diversity (O'Toole & Raw, 1991; Petanidou & Ellis, 1993; Michener, 2000; Petanidou & Lamborn, 2005), which in turn is associated with high nectar niche diversity, especially in low scrub systems (Potts et al., 2004). Because very few Mediterranean species secrete copious nectar, with the majority producing relatively little, invasions by bumblebees will affect the diversity of medium- to long-tongued solitary bees negatively, as has happened in Israel (Dafni & Shmida, 1996). Similarly, under the pressure of intense beekeeping it is expected that the diversity of solitary bees as a whole will decline. Introduced bees are widespread, and because of this, deleterious effects are expected to occur on a large scale, and in some areas may be irretrievably severe. In this respect, areas managed almost solely by uncontrolled grazing (or rather, overgrazing) and intense beekeeping, especially in the East Mediterranean, are a priority risk (Rackham & Moody, 1992; Petanidou et al., 2001). They encompass not only marginal and wild habitats, but also abandoned agricultural lands, frequently terraced slopes, and hills that are nowadays unprofitable for primary production. That these areas are frequently isolated, and often on islands, may be an even worse omen (Roubik & Wolda, 2001).

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