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SUGARS IN MEDITERRANEAN FLORAL NECTARS: AN ECOLOGICAL AND EVOLUTIONARY APPROACH

THEODORA PETANIDOU*

Laboratory of Biogeography and Cultural Ecology, Department of Geography, University of the Aegean, University Hill, GR-81100 Mytilene, Greece

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Abstract—High-pressure liquid chromatography analyses of 73 plant species showed that the nectars of phrygana (East Mediterranean garrigue) mainly contain sucrose, glucose, and fructose, and traces of 10 minor sugars. Although the sucrose/hexose ratio was not related to plant life habit, ecological constraints had a detectable effect in shaping sugar composition. This was detected by distinguishing the phryganic plant species into "spring–summer" and "winter" flowering, with the distinction made on the basis of the water deficit in the study area. Plants flowering in spring–summer had a higher rate of "high sucrose" (i.e., sucrose/hexose ratio $\geq$0.5; 60.8% of the plant species) vs. "low hexose" nectars (i.e., ratio <0.5; 39.2%). The ratio was reversed in winter flowering species (36.4% vs. 63.6% with "high sucrose" and "high hexose," respectively). Sucrose/hexose ratios were associated with plant family. The highest values were those of Lamiaceae, which differed significantly from the "low sucrose" Liliaceae and Apiaceae. Based on recorded plant–pollinator interactions in the community, the present data provide evidence of a partitioning of nectar resources by the existing pollinator guilds within the community, based on the sugar profiles of nectar (all sucrose/hexose ratios for all interactions). Among all major groups, bees and wasps (aculeates) preferred "high sucrose" nectars, which differed significantly from syrphids, anthomyid a.o. flies, and beetles that visited "low sucrose" nectars. Similarly, butterflies visited "lower sucrose" nectars compared to bees. Within families, only Megachilidae could be clearly characterized as "high sucrose" consumers, differing in this respect from all the remaining insect groups including most other bee families. This confirms previous findings that Megachilidae have a key position in Mediterranean

* To whom correspondence should be addressed. E-mail: t.petanidou@aegean.gr

communities where they probably constitute a selective factor for "high sucrose" nectars.

Key Words—Nectar sugars, sugar ratio, sucrose, glucose, fructose, hexoses, sugar preference, evolutionary constraints, bees, Megachilidae, phrygana, Mediterranean ecosystems, pollination ecology.

INTRODUCTION

Among the major rewards to pollinators, floral nectar is unique, and likely subject to selection pressures that result in nectar differences among closely related plants pollinated by different animals (Pyke and Waser, 1981; Baker and Baker, 1982). The literature on floral nectars is considerable. Amount and sugar concentration of nectars are related to pollinator type (Percival, 1961, 1965; Baker and Baker, 1975), especially the hexose/sucrose ratio (Wykes, 1952; Percival, 1961; Baker and Baker, 1979, 1982, 1983, 1990; Southwick, 1982; Stiles and Freeman, 1993; Petanidou et al., 1996). Amino acids in nectars have also received attention, especially their significance to pollinators (Gottsberger et al., 1984; Baker and Baker, 1986; Petanidou et al., 1996; Petanidou, unpublished data).

Several large-scale studies have focused on the relative concentration of sugar components of nectar. In her pioneering, semiquantitative study on nectar of 889 species, Percival (1961) distinguished sucrose-dominant, balanced sugar, and hexose dominant nectars, which she found related to plant family affinity as well as to pollinator type (Percival, 1965). Baker and Baker (1982, 1990) confirmed Percival's results corroborating the correlation between tubular flowers and sucrose richness, and the tendency of open flowers to be hexose-rich. They further placed the sugar profile into a coevolutionary context, by also considering the plant's pollination mode, referred to as the "pollination syndrome." Based on the nectar analysis of 765 species of different origin, they found that the sugar profile [measured in weight as sucrose/hexose ratio: S/(G + F)] could be associated with the plant's pollination syndrome: plants with sucrose-dominant (>0.999) and sucrose-rich (0.999–0.500) nectars are pollinated by hummingbirds, butterflies, and long-tongued bees, whereas plants with hexose-rich (0.499–0.100) and hexose-dominant (<0.100) nectars are pollinated by short-tongued bees and flies. In another study focusing on a wide range of hummingbird-visited plants in Costa Rica, Stiles and Freeman (1993) found that the sucrose concentration of floral nectars decreased with elevation while fructose concentration increased. All the above results were based on the assumption that a plant is pollinated by a certain insect group, and have not been tested by considering the actual response of the pollinators, i.e., all plant–pollinator interactions observed in the community. However, it is commonly

known that actual pollinators may differ from those suggested by the pollination syndrome, and most plants receive visits of a large array of pollinators.

Little is known of the nectar composition of Mediterranean plants, and certainly not at the community level (Dafni et al., 1988; Petanidou et al., 1996, 2000). Due to water shortage in Mediterranean communities, several aspects of pollination ecology are influenced by climate, such as nectar quantity and concentration (Herrera, 1985; Petanidou and Vokou, 1990; Petanidou and Smets, 1995), flower and nectary structure (Petanidou et al., 2000), pollen calorific value (Petanidou and Vokou, 1990), flowering time (Petanidou and Vokou, 1993; Petanidou et al., 1995), and pollinator assemblages (Petanidou and Ellis, 1993, 1996).

In this work, I investigated the role of nectar sugars in phrygana (East Mediterranean garrigue community). In these communities, pollinator assemblages are not as variable as in other arid, tropical, and temperate systems (no birds, no bats, few bumblebees), with the majority of plants being pollinated by wild bees (Petanidou and Ellis, 1993, 1996; Petanidou and Potts, 2005). As this is the first community study from the area, my specific questions were: (1) What sugars dominate in the Mediterranean nectars? (2) What are the major constraints shaping nectar sugar ratios (phylogenetic, ecological, coevolutionary): Are nectar sugar ratios related to plant family (phylogenetic constraints, as found by Percival, 1961) and pollinator assemblages (coevolutionary constraint, as previously concluded by Percival (1965), Baker and Baker (1983), and Stiles and Freeman (1993)), or do plant flowering period and/or life habit also matter (ecological constraints), as it is normally the case with other pollination characteristics in the Mediterranean?

I carried out the investigation in a typical phrygana, and considered all nectariferous plants occurring in the phryganic community (30 ha) for which nectar collection was practical, with flowering times dispersed throughout the year. As all species were native and typical for the phrygana, this allowed me to explore the effect of ecological constraints. In addition, the large number of plants studied (73) allowed investigation within plant families (phylogenetic constraints). Previous studies within the same community allowed me to use a detailed plant–pollinator database to explore any coevolutionary effects. The latter approach, i.e., matching the nectar sugar composition and the response of pollinator assemblages based on plant–pollinator interactions at a community level, is novel.

METHODS AND MATERIALS

Study Site, Plant Species, and Field Measurements. I studied the nectar of 73 phryganic species occurring in the nature reserve of the “I. and A. Diomedes

Botanical Garden of Athens University" located 10 km west of the center of Athens, Greece. The site and the phryganic community have been described in earlier studies conducted by Petanidou and Ellis (1993, 1996) and Petanidou et al. (1995).

Nectar volume, flower depth, and other measurements used in this study were taken from Petanidou and Smets (1995). Nectar for laboratory analyses was collected from flowers selected at random using the same plants from which nectar volume was measured. All flowers used were at their first day of anthesis, covered in bud stage with bridal veil on the eve of the collection day to prevent nectar removal by insects. Nectar was collected the following day, always towards noon to early afternoon (1100–1400 hr) except for *Capparis spinosa* sampled between 0930 and 1000 hr. The nectar of each flower was picked up directly on a Whatman No. 1 small paper wick and fixed on a stainless steel pin that had been cleaned with acetone. The paper wicks, placed on styrofoam blocks, were left to air-dry. They were stored in airtight containers over silica gel until analysis. Touching with the fingers or other possible contaminating means was carefully avoided (Petanidou et al., 1996).

Nectar Analysis. Sugar analysis was carried out with high-pressure liquid chromatography (HPLC) (Dionex, Sunnyvale CA, USA). Before analysis, the nectar content of each wick was dissolved in 1 ml of distilled water in a microcentrifuge tube by intermittent vortexing at room temperature for at least 1 hr. Tubes were centrifuged to remove paper particles (Petanidou et al., 1996). Analysis was made directly on a CarboPac PA1 anion-exchange column, and quantified by a pulsed amperometric detector. Flow rate was 1 ml min^{-1}. The elution conditions were 100 mM NaOH for 4 min, a linear gradient from 0 to 30 mM Na acetate in 100 mM NaOH over 16 min, a linear gradient of 30–100 mM Na acetate in 100 mM NaOH over 30 min, and finally 300 mM NaOH for 10 min. The column was regenerated with 1 M NaOH for 10 min and equilibrated for 20 min with starting buffer after every run. I investigated the presence of 15 sugars, viz. glucose, fructose, sucrose, sorbitol, mannitol, ribose, melibiose, maltose, stachyose, arabinose, mannose, rhamnose, lactose, trehalose, and gentiobiose, all of which have been reported to occur in floral nectars (cf. review by Baker and Baker, 1983). I did not consider xylose, which is present in specific nectars of the South African species of *Protea* and *Faurea* (Nicolson and Van Wyk, 1998). Sugar quantification was performed on the peak areas by comparison with external standards.

Flower Visitors. In order to detect whether pollinator species had a differential response to the different sugar contents of flowers, I used the community data matrix from Petanidou (1991), which was also used as a basis for Petanidou and Vokou (1993), Petanidou and Ellis (1996), and Petanidou and Potts (2005). This matrix contained plant–pollinator interactions for 70 of the 73 plant species analyzed. All flower visitors were considered pollinators if they

visited the flowers repeatedly irrespective of their "quality" (pollinator efficiency). This is normally done in such community studies (Waser and Ollerton, 2005). Excluded from the analyses were *Echinops sphaerocephalus* subsp. *albidus* and *Teucrium chamaedrys* for which there were no pollinator data, as well as *Romulea linaresii*, which was not visited by insects. The 70 plant species were visited by 576 insect species, resulting in 1930 plant–pollinator interactions.

The families Andrenidae, Halictidae, and Colletidae were considered collectively to comprise of short-tongue bee species, whereas the families Anthophoridae, Apidae, and Megachilidae were composed of long-tongue ones (Petanidou and Ellis, 1996; Michener, 2000).

Data Analysis. Values from all laboratory analyses were calculated per flower. This was the average of several separate runs (3–11, except in a few cases), each one on the basis of one flower where nectar secretion was sufficient (e.g., Lamiaceae). In cases where nectar secretion per flower was low, samples were pooled for HPLC analysis.

I used the same sucrose/hexose ratio as Baker and Baker in all their papers: sucrose/(glucose + fructose), all sugar amounts calculated in weights (Baker and Baker, 1983). Differences among plant families in sucrose/hexose ratios were tested using one-way ANOVAs. Seven plant families were considered in the analysis aiming to explore any phylogenetic affinity of nectar composition. Apart from being the most species-rich in the phryganic community (with ≥ 3 plant species), the plant families considered in the data analysis should not be closely related in terms of their phylogenetic history, the independence control based on the plant evolution tree appearing in Dodd et al. (1999), which is enriched with pollination mode data. The families tested were Boraginaceae, Asteraceae, Lamiaceae, Fabaceae, Liliaceae, Apiaceae, and Ranunculaceae, whereas the remaining families were treated as a separate eighth group. The family Dipsacaceae, represented by three species in the study phrygana, does not appear in the tree by Dodd et al. (1999); thus, it was treated together with the remaining species of the eighth group. Similarly, differences among insect groups in their response to flowers was explored by comparing the nectar sugar ratios of the plant species visited by all species of the insect group, considering all ratio values of all plant–pollinator interactions.

In order to investigate the importance of flowering time in shaping nectar composition, I considered the differential water regime (i.e., the relative evapotranspiration vs. rainfall) throughout the year. According to the data taken from ombrothermic curves of the area (cf. Petanidou and Ellis, 1993), two periods were distinguished: (1) April 1–September 15, when evapotranspiration exceeds rainfall, and (2) September 16–March 31, when rainfall exceeds evapotranspiration. Plant species having their midpoint of flowering in either period were assigned as "spring–summer" or "winter" flowering species.

TABLE 1. PLANT SPECIES STUDIED FOR THEIR NECTAR SUGARS BY HPLC[a]

Date of nectar collection	Plant species	Abbreviation	Life form	Nectar volume (μl flower^{-1})	Flower depth (mm)	Midpoint of flowering (calendar day)
Amaryllidaceae						
21.10.92	*Sternbergia lutea* Orph. ex Nym. subsp. *sicula* (Tin. ex Guss.) D.A. Webb	Sg	geo	1.33	10.4	297
Apiaceae						
16.7.92	*Eryngium campestre* L.	Ey	herb	0.00	1.9	193
7.4.92.	*Scandix australis* L. subsp. *australis*	Sc	ther	0.03	0.0	73
4.6.92	*Thapsia garganica* L.	Tg	herb	0.02	0.0	136
9.4.92	*Tordylium apulum* L.	Ta	ther	0.01	0.0	105
Asteraceae						
13.4.93	*Calendula arvensis* L.	Ca	ther	0.01	3.6	80
14.6.93	*Centaurea orphanidea* Heldr. & Sart. ex Boiss. subsp. *orphanidea*	Co	ther	0.01	11.2	165
25.4.92	*Centaurea raphanina* Sibth. & Sm. subsp. *mixta* (DC.) Runemark	Cr	herb	0.21	21.6	117
3.5.92	*Chrysanthemum coronarium* L.	Cc	ther	0.01	4.3	128
13.7.92	*Echinops microcephalus* Sibth. & Sm.	Ec	herb	0.13	7.4	190
9.8.92	*Echinops sphaerocephalus* L. subsp. *albidus* (Boiss. & Spruner) Kozuharov	Es	herb	0.16	7.4	220
2.6.92	*Helichrysum stoechas* DC. subsp. *barrelieri* (Ten.) (Nyman)	Hs	frut	0.00	4.4	136
26.4.92	*Hypochaeris achyrophorus* L.	Ha	ther	0.01	3.5	114

4.6.92	*Pallenis spinosa* (L.) Cass.		Ps	ther	0.00	2.2	144
1.5.92	*Phagnalon graecum* Boiss. & Heldr.		Pg	frut	0.15	4.7	125
28.4.92	*Reichardia picroides* (L.) Roth		Rp	herb	0.03	8.3	107
1.5.92	*Tragopogon porrifolius* L. subsp. *porrifolius*		Tp	ther	0.01	7.7	110
Boraginaceae							
7.4.92	*Alkanna tinctoria* (L.) Tausch		At	herb	0.34	4.9	95
13.4.93	*Anchusa variegata* (L.) Lehm.		Av	ther	0.45	6.2	62
3.6.92	*Echium creticum* L.		Ea	herb	2.89	6.9	178
12.7.92	*Heliotropium europaeum* L.		He	ther	0.05	2.0	276
13.7.92	*Heliotropium hirsutissimum* Grauer		Hh	ther	0.06	4.6	277
Brassicaceae							
19.4.93	*Eruca vesicaria* Cav. subsp. *sativa* (Mill.) Thell.		Ev	ther	0.13	9.2	113
2.5.92	*Sisymbrium orientale* L.		So	ther	0.01	3.2	119
Campanulaceae							
27.4.92	*Campanula drabifolia* Sibth. & Sm. subsp. *drabifolia*		Cf	ther	0.03	6.0	118
Capparidaceae							
13.6.94	*Capparis spinosa* L. var. *inermis* Turra	Cs		frut	42.05	6.2	188
Caryophylaceae							
25.4.92	*Petrorhagia velutina* (Guss.) P.W. Ball & Heywood	Pv		ther	0.04	16.0	106
9.4.92	*Silene colorata* Poir.	Si		ther	0.06	5.9	95

TABLE 1. CONTINUED

Date of nectar collection	Plant species	Abbreviation	Life form	Nectar volume (μl flower^{-1})	Flower depth (mm)	Midpoint of flowering (calendar day)
Cistaceae						
30.4.92	*Cistus parviflorus* Lam.	Cp	frut	0.05	0.0	125
2.5.92	*Cistus salvifolius* L.	Ci	frut	0.02	0.0	104
Convolvulaceae						
13.7.92	*Convolvulus arvensis* L.	Cv	herb	0.05	2.5	170
8.7.92	*Convolvulus cantabrica* L.	Cn	herb	0.06	2.5	169
Cucurbitaceae						
15.7.92	*Ecballium elaterium* (L.) A. Rich.	Ee	herb	0.03	0.7	214
Dipsacaceae						
5.6.92	*Pterocephalus papposus* (L.) Coult.	Pp	ther	0.03	5.3	123
12.5.93	*Scabiosa atropurpurea* L.	Sa	ther	0.01	4.5	125
27.4.92	*Tremastelma palaestinum* (L.) Janch.	Tm	ther	0.05	5.7	116
Ericaceae						
1.11.93	*Erica verticillata* Forssk.	En	frut	0.00	3.6	363
Euphorbiaceae						
11.4.93	*Euphorbia acanthothamnos* Heldr. & Sart. ex Boiss.	Eu	frut	0.25	0.0	79
Fabaceae						
16.5.93	*Anthyllis hermanniae* L.	Ah	frut	0.01	3.1	132
8.4.92	*Astragalus monspessulanus* L.	Ao	herb	0.28	10.4	102
17.4.93	*Hymenocarpos circinnatus* (L.) Savi	Hc	ther	0.01	1.9	96
29.4.92	*Psoralea bituminosa* L.	Pso	herb	0.24	7.8	135
8.4.92	*Trifolium stellatum* L.	Ts	ther	0.04	8.3	98

Globulariaceae						
11.4.93	*Globularia alypum* L.	Ga	frut	0.01	4.5	77
Iridaceae						
17.11.92	*Crocus cancellatus* Herb.	Ce	geo	0.19	92.0	298
25.2.94	*Romulea linaresii* Parl. subsp. *graeca* Bég.	Ro	geo	0.07	5.7	33
Lamiaceae						
11.6.93	*Ballota acetabulosa* (L.) Benth.	Ba	herb	0.14	8.6	160
26.2.94	*Lamium amplexicaule* L. subsp. *amplexicaule*	La	ther	0.20	14.6	74
15.5.93	*Phlomis fruticosa* L.	Pf	frut	2.52	16.1	108
28.4.92	*Prasium majus* L.	Pm	frut	7.48	9.8	114
14.4.93	*Salvia triloba* L.f.	St	frut	7.74	11.9	94
9.4.92	*Salvia verbenaca* L.	Sb	ther	0.33	7.1	85
16.5.93	*Satureja thymbra* L.	Sj	frut	0.05	7.6	137
2.6.92	*Stachys cretica* L. subsp. *cretica*	Sy	herb	0.59	7.4	137
5.6.92	*Teucrium chamaedrys* L.	Td	frut	0.50	7.9	135
4.6.92	*Teucrium polium* L. subsp. *capitatum* (L.) Arcang.	Te	frut	0.06	4.2	156
8.7.92	*Thymus capitatus* (L.) Hoffmanns. & Link	Tc	frut	0.10	5.4	171
Liliaceae						
30.4.92	*Allium subhirsutum* L.	Ab	geo	0.03	0.0	106
20.10.92	*Asparagus acutifolius* L.	Af	geo	0.02	0.0	268
6.4.92	*Asphodelus aestivus* Brot.	Am	geo	2.44	3.8	85
25.2.94	*Fritillaria graeca* Boiss. & Spruner subsp. *graeca*	Fg	geo	0.06	24.2	85
24.2.94	*Muscari commutatum* Guss.	Mu	geo	0.01	5.5	54
24.2.94	*Muscari neglectum* Guss. ex Ten.	Mn	geo	0.01	4.8	39

TABLE 1. CONTINUED

Date of nectar collection	Plant species	Abbreviation	Life form	Nectar volume (μl flower^{-1})	Flower depth (mm)	Midpoint of flowering (calendar day)
14.4.93	*Ornithogalum exscapum* Ten. *O. graecum* C. Zahariadi	Oc	geo	0.05	0.0	70
21.10.92	*Scilla autumnalis* L.	Su	geo	0.01	0.0	290
6.9.92	*Urginea maritima* (L.) Baker	Um	geo	0.64	0.0	261
Malvaceae						
5.6.92	*Alcea pallida* (Willd.) Waldst. & Kit.	Ap	herb	2.54	0.0	160
Ranunculaceae						
10.7.92	*Delphinium peregrinum* L.	Dp	ther	0.52	16.0	185
5.6.92	*Nigella arvensis* L.	Ng	ther	0.30	3.3	169
13.4.92	*Ranunculus sprunerianus* Boiss.	Ra	geo	0.08	1.4	98
Resedaceae						
27.4.92	*Reseda alba* L.	Re	herb	0.10	0.0	104
Rutaceae						
5.6.92	*Ruta graveolens* L.	Rg	herb	0.32	0.0	145
Thymelaeaceae						
27.2.93	*Thymelaea hirsuta* (L.) Endl.	Th	frut	0.00	2.9	25

[a] Life forms are: geophytes (geo), therophytes or annuals (ther), herbaceous perennials (herb), frutescent or woody perennials (frut). Life form, flower depth, nectar volume, and midpoint of flowering are after Petanidou et al. (1995) and Petanidou and Smets (1995). Nomenclature used is according to The International Plant Names Index (2004).

Before any statistical application, the data were tested for normality, and if not normally distributed, nonparametric tests were applied (Kruskal–Wallis ANOVA, Spearman *R* correlation). When necessary, Kruskall–Wallis ANOVAs were followed by posthoc Mann–Whitney *U* tests and application of the ultra conservative Bonferroni correction (Pagano and Gauvreau, 1993). Whenever used, mean values are followed by their SEs.

RESULTS

Table 1 contains the list of all 73 plant species, with some floral attributes possibly related to sugars contained in the nectars. All 13 sugars used as references in the HPLC analyses were found in the nectars of phrygana flowers, and some additional unknown peaks were also found (Table 2). As expected, the most common sugars were the "big three": glucose, fructose, and sucrose (Baker and Baker, 1983). The remaining 10 contributed little to the sugar profile of phryganic nectars. Among these, sorbitol had the most significant contribution in a few cases with >1% in total nectar sugars, followed by mannose and melibiose.

Based on the % of sucrose contained in the total nectar sugars (in nmol) and the sucrose/hexose ratios (in weight), the phryganic plant families can be distinguished into three groups: the first with "high sucrose" nectars (Ranunculaceae, Lamiaceae, Fabaceae), a second with "low sucrose" nectars (Apiaceae, Liliaceae), and a third, mixed group, encompassing Asteraceae, Boraginaceae, and the remaining families (Table 3). No plant family has a close phylogenetic relationship to any other family within the same or different group (Dodd et al., 1999).

Plant families differed in their sucrose/hexose ratios (K–W $H_{(7,73)} = 35.6$; $P < 0.001$; Table 3). *A posteriori* comparisons showed that these differences were due to the higher ratios of Lamiaceae (M–W *U* tests after applying Bonferroni correction, $P = 0.006$ and $P = < 0.001$, for the pairs Lamiaceae–Liliaceae and Lamiaceae–other families, respectively). The results are the same if the outlier *Anthyllis hermanniae* is not considered.

The values of the sucrose/hexose ratios were related to flower depth (Spearman rank $R = 0.394$, $P < 0.001$; Figure 1) and nectar volume ($R = 0.383$, $P < 0.001$), especially when the outlier *A. hermanniae* was not considered ($R = 0.441$, $P < 0.001$; $R = 0.426$, $P < 0.001$, respectively). (Being an outlier, this species is considered separately or not at all in the statistical analyses.)

The sucrose/hexose ratio was not time-dependent (Spearman *R* correlation against midpoint of flowering, $P = 0.749$). However, when considering "spring–summer" and "winter" species flowering within different water regimes (see "Data Analyses" in METHODS AND MATERIALS), I found

TABLE 2. SUGAR COMPOSITION DATA OF THE NECTARS OF THE PHRYGANIC PLANTS[a]

Plant species	N	Glucose	Fructose	Sucrose	Sorbitol	Mannitol	Ribose	Melibiose	Maltose	Stachyose	Arabinose	Mannose	Lactose	Trehalose	Unknown sugars	% Contribution to the total sugars		S: (G + F) (in weight)
		(nmol flower^{-1})														Minor sugars	Sucrose	
Sg	8 (3)	313 ± 91.4	319 ± 73.7	289 ± 73.3	11 ± 2.4										28 ± 12.3	4.0	30.1	0.87
Ey	12 (1)	113	142	12											8	2.9	4.2	0.09
Sc	9 (4)	148 ± 42.0	121 ± 31.9	52 ± 14.1	1 ± 0.3											0.3	16.1	0.37
Tg	5 (3)	513 ± 72.3	689 ± 84.3	20 ± 6.3												0.0	1.6	0.03
Ta	15 (4)	50 ± 1.5	58 ± 2.8	17 ± 2.6	0.4 ± 0.2							0.3 ± 0.1				0.6	13.3	0.29
Ca	12 (3)	50 ± 21.6	52 ± 19.3	3 ± 0.9												0.0	3.2	0.06
Co	13 (4)	12 ± 2.6	8.1 ± 2.2	110 ± 57.6												0.0	84.7	10.51
Cr	11 (3)	62 ± 5.1	15 ± 3.3	491 ± 100.2												0.0	86.5	12.20
Cc	24 (5)	58 ± 24.4	50 ± 16.8	4 ± 0.9	6 ± 1.2											5.4	3.0	0.06
Ec	8 (5)	443 ± 71.8	1201 ± 100.4	10 ± 2.9				11 ± 3.0								0.7	0.6	0.01
Es	4 (4)	285 ± 50.9	281 ± 44.3	188 ± 59.0											3 ± 0.9	0.3	25.0	0.64
Hs	40 (4)	31 ± 3.8	38 ± 5.9	33 ± 12.5				0.2 ± 0.1								0.2	31.9	0.89
Ha	51 (3)	104 ± 66.4	111 ± 73.5	4 ± 2.5				1 ± 0.6								0.5	1.8	0.03
Ps	18 (2)	4 ± 1.2	2 ± 0.8	1 ± 0.3												0.0	15.0	0.34
Pg	12 (1)	58	63	3												0.0	2.4	0.05
Rp	20 (3)	78 ± 44.4	78 ± 32.4	46 ± 18.9												0.0	22.8	0.56
Tp	14 (3)	168 ± 54.1	185 ± 54.4	40 ± 15.9				1 ± 0.4								0.3	10.2	0.22
At	6 (4)	421 ± 94.8	148 ± 50.3	567 ± 119												0.0	49.9	1.89
Av	13 (5)	216 ± 59.7	130 ± 44.0	385 ± 81.3					0.5 ± 0.1	0.4 ± 0.1	1 ± 0.0					0.3	52.5	2.11
Ea	5 (5)	652 ± 80.3	157 ± 44.8	3684 ± 540.7												0.0	82.0	8.65
He	8 (3)	134 ± 51.8	137 ± 62.8	15 ± 4.3												0.0	5.1	0.10
Hh	8 (3)	146 ± 65.3	153 ± 59.5	188 ± 67.9												0.0	38.6	1.19
Ev	5 (3)	469 ± 82.8	483 ± 88.9	4 ± 1.6												0.0	0.4	0.01
So	5 (3)	283 ± 56.4	315 ± 77.8	5 ± 0.9											8 ± 3.1	1.3	0.8	0.02
Cf	6 (3)	308 ± 73.8	357 ± 35.8	529 ± 84.4												0.0	44.3	1.51
Cs	5 (5)	27972 ± 8486.2	27242 ± 9269.9	15098 ± 4295.8												0.0	21.5	0.52
Pv	8 (2)	376 ± 77.4	435 ± 109.4	4 ± 2.0	2 ± 0.9			5 ± 2.0								0.8	0.5	0.01
Si	4 (4)	91 ± 22.3	85 ± 22.3	3 ± 1.1												0.0	1.4	0.03
Cp	10 (3)	763 ± 50.8	806 ± 22.8	1820 ± 149.9	4 ± 1.0											0.1	53.7	2.20
Cl	10 (3)	1442 ± 100.9	1628 ± 201.8	578 ± 72.3	31 ± 7.8							22 ± 5.3				1.4	15.6	0.36
Cv	6 (3)	325 ± 72.7	368 ± 79.7	204 ± 62.9	22 ± 4.6											2.4	22.2	0.56

Cn	10 (4)	293 ± 63.9	336 ± 50.1	10 ± 3.8	11 ± 3.2									1.7	1.5	0.03
Ee	14 (3)	47 ± 14.6	47 ± 15.2	69 ± 9.3										0.0	42.3	1.39
Pp	14 (2)	151 ± 69.1	155 ± 73.0	128 ± 53.7										0.0	29.5	0.79
Sa	8 (3)	155 ± 50.2	157 ± 49.9	48 ± 13.2										0.0	13.3	0.29
Tm	24 (3)	147 ± 14.3	166 ± 10.6	69 ± 7.0										0.0	18.1	0.42
En	6 (5)	5 ± 0.9	5 ± 0.9	0										0.0	0.0	0.00
Eu	14 (2)	84 ± 7.9	111 ± 16.3	21 ± 4.6		0.3 ± 0.1	4 ± 1.6						6 ± 1.7	4.4	9.2	0.20
Ah	11 (4)	0.3 ± 0.1	0.3 ± 0.1	41 ± 15.0										0.0	98.5	121.75
Ao	13 (6)	265 ± 36.7	25 ± 5.5	898 ± 174.8			2 ± 0.1		1 ± 0.0	0.1 ± 0.0				0.2	75.4	5.88
Hc	13 (2)	30 ± 7.2	34 ± 8.3	35 ± 12.6	0.4 ± 0.2	0.4 ± 0.2								0.7	34.9	1.03
Pso	15 (3)	40 ± 6.8	49 ± 7.3	618 ± 192.8										0.0	87.4	13.21
Ts	3 (3)	78 ± 37.0	89 ± 42.0	78 ± 56.4										0.0	31.8	0.89
Ga	6 (1)	51	35	17										0.0	16.4	0.37
Ce	13 (3)	218 ± 23.2	210 ± 11.1	109 ± 12.4								0.3 ± 0.0		0.1	20.3	0.48
Ro	4 (4)	155 ± 47.1	180 ± 57.4	41 ± 13.1										0.0	11.0	0.23
Ba	10 (10)	47 ± 18.0	11.9 ± 4.7	279 ± 61.8										0.0	82.7	9.05
La	4 (4)	68 ± 11.6	14 ± 2.7	120 ± 23.6										0.0	59.3	2.77
Pf	10 (10)	266 ± 48.6	1258 ± 232.9	2559 ± 518.4										0.0	62.7	3.19
Pm	9 (9)	980 ± 190.9	267 ± 68.3	3653 ± 852.5										0.0	74.6	5.57
St	5 (5)	974 ± 281.2	1407 ± 430.9	4233 ± 1289.6										0.0	64.0	3.38
Sb	7 (7)	244 ± 69.1	109 ± 32.5	399 ± 93.0										0.0	53.1	2.15
Sj	6 (6)	62 ± 27.5	97 ± 35.6	232 ± 72.4										0.0	59.3	2.77
Sy	10 (10)	155 ± 93.5	384 ± 153.4	1509 ± 283.7										0.0	73.7	5.32
Td	3 (3)	559 ± 84.7	692 ± 88.4	2011 ± 101.0										0.0	61.6	3.05
Te	10 (10)	116 ± 42.4	349 ± 76.9	775 ± 86.5										0.0	62.4	3.16
Tc	8 (8)	51 ± 9.0	176 ± 17.7	121 ± 13.7										0.0	34.8	1.01
Ab	10 (3)	122 ± 64.9	125 ± 66.3	53 ± 7.5										0.0	17.6	0.41
Af	55 (6)	93 ± 34.8	127 ± 47.4	1 ± 0.6				0.3 ± 0.1	0.1 ± 0.0					0.2	0.5	0.01
Am	3 (3)	7844 ± 601.3	8035 ± 702.8	5446 ± 507.7										0.0	25.5	0.65
Fg	1	18	175	112										0.0	36.7	1.10
Mu	11 (11)	68 ± 12.7	51 ± 14.9	2 ± 0.8										0.0	1.5	0.03
Mn	11 (11)	116 ± 21.8	134 ± 26.7	2 ± 1.4										0.0	0.8	0.02
Oc	3 (3)	262 ± 36.6	123 ± 10.2	8 ± 3.2										0.0	2.0	0.04
Su	8 (3)	83 ± 29.2	82 ± 31.4	0										0.0	0.0	0.00
Um	4 (4)	1376	1041 ± 179.5	0				11 ± 2.1						0.5	0.0	0.00
Ap	3 (3)	10,456 ± 2002.4	11,351 ± 2025.5	831 ± 88.0										0.0	3.7	0.07

TABLE 2. CONTINUED

Plant species	N	Glucose	Fructose	Sucrose	Sorbitol	Mannitol	Ribose	Melibiose	Maltose	Stachyose	Arabinose	Mannose	Lactose	Trehalose	Unknown sugars	% Contribution to the total sugars		S: (G + F) (in weight)
		(nmol flower^{-1})														Minor sugars	Sucrose	
Dp	10 (3)	13 ± 6.7	76 ± 51.7	798 ± 35.0		4 ± 1.0							2 ± 0.7		5 ± 1.4	1.3	88.8	17.05
Ng	3 (3)	3 ± 1.0	27 ± 7.2	287 ± 55.7	3 ± 1.2	2 ± 0.9										1.4	89.1	17.89
Ra	5 (3)	76 ± 31.7	75 ± 32.4	643 ± 102.9												0.0	80.9	8.06
Re	5 (3)	457 ± 80.3	436 ± 69.2	390 ± 73.4												0.0	30.4	0.83
Rg	8 (3)	1146 ± 301.3	2047 ± 704.2	225 ± 65.6					26 ± 9.3						62 ± 17.9	2.5	6.4	0.13
Th	10 (2)	2 ± 1.3	2 ± 0.8	4 ± 1.5												0.0	47.2	1.70

N is the total number of flowers analyzed by HPLC, the number of runs given in parentheses. Plant abbreviations are given in Table 1.

[a] Data columns are amounts of different nectar sugars (nmol flower^{-1} ± SE); contribution (%) of sucrose and of the minor sugars (=all but the "big three") in the nectar (in nmol); sucrose/hexose ratio (calculated on a weight basis).

TABLE 3. SUMMARY VALUES OF THE PLANT FAMILIES IN THE COMMUNITY[a]

	N	% Sucrose over total sugars (nmol)	S/(G + F) (in weight)
High sucrose families			
Lamiaceae	11	62.5 ± 3.76	3.8 ± 0.65
Ranunculaceae	3	86.3 ± 2.68	14.3 ± 3.15
Fabaceae	5	65.6 ± 13.67	28.6 ± 23.41
Families with mixed floral nectars			
Asteraceae	12	23.9 ± 8.84	2.1 ± 1.25
Boraginaceae	5	45.6 ± 12.41	2.8 ± 1.51
Other	21	18.0 ± 3.78	0.6 ± 0.14
Dipsacaceae	3	20.3 ± 4.79	0.5 ± 0.15
Low sucrose families			
Apiaceae	4	8.8 ± 3.49	0.2 ± 0.08
Liliaceae	9	9.4 ± 4.60	0.3 ± 0.13

[a] Data columns are: number of plant species per family (N); % sucrose content calculated on the basis of nmoles contained in the nectar; and sucrose/hexose ratio (mean±SE) calculated on the basis of sugar (S, G, F) weights.

significant differences between these two groups in both sucrose/hexose ratio (M–W $U_{(51,22)} = 366.0$; $P = 0.019$) and sucrose content (M–W $U_{(51,22)} = 367.0$; $P = 0.017$). Among the "spring–summer" species, 60.8% have "high sucrose" nectars vs. 39.2% with "high hexose" nectars (Tables 1 and 2). The picture is

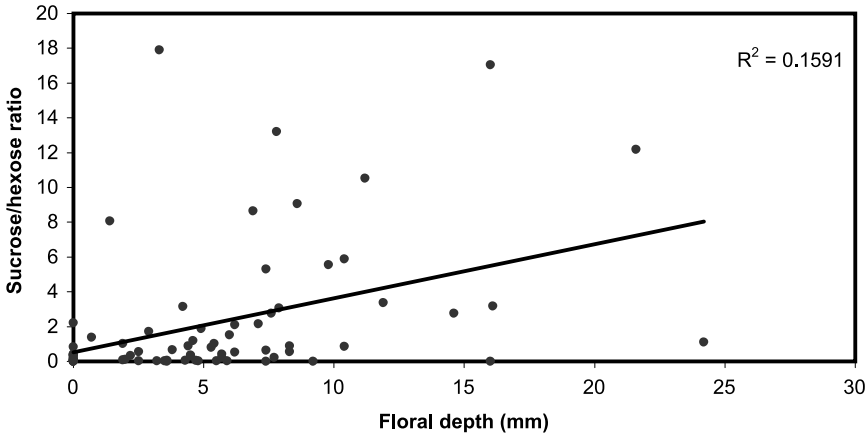

FIG. 1. Sucrose/hexose ratio represented against floral depth of the plant species studied. Best-fitted line and R^2 value are displayed on the chart. *Anthyllis hermanniae* (ratio outlier) and *Crocus cancellatus* (depth outlier) were excluded.

reversed during the wet period of the year, with 36.4% of the "winter" plants having "high sucrose" and 63.6% having "high hexose" nectars. There was no difference in sucrose/hexose ratio among plants of different life habit (K–W $H_{(3,72)} = 6.454$; $P = 0.092$).

The response of pollinator groups to nectar sucrose/hexose ratios is summarized in Tables 4 and 5. The tables give the average value of sugar ratios calculated over the species of plants visited by all insect species on the basis of all interactions observed between them in the community. Among all major insect groups, bees and wasps (aculeates) show the highest preference for high-sucrose nectars. Lepidoptera, a rather heterogeneous group, scored between bees (high) and flies (low). Among bee families, the greatest preference for high-sucrose nectar was shown by the Megachilidae, then by the Anthophoridae, followed by a third group encompassing Halictidae, Colletidae, and Apidae, and finally the Andrenidae family, which has the lowest preference. There was a significant difference in the preference for sugar profiles of nectar among the major insect groups at the level of superfamilies–orders (Table 4; ANOVA, outlier *Anthyllis* excl.: $F_{(6,1917)} = 15.63$; $P < 0.001$). The difference was equally high when major groups are broken down into families of high relevance to pollination (Table 5; $F_{(16,1907)} = 10.64$; $P < 0.001$). *A posteriori* tests (Tukey HSD test) showed that the difference between superfamilies–orders were due to bees (Apoidea–Coleoptera: $P < 0.001$; Apoidea–Diptera: $P < 0.001$; Apoidea–Lepidoptera: $P = 0.048$; Apoidea–Syrphidae: $P < 0.001$) and to aculeates (Aculeata–Coleoptera: $P = 0.001$; Aculeata–Diptera: $P < 0.001$; Aculeata–

TABLE 4. SUCROSE/HEXOSE RATIOS OF THE FLORAL NECTARS VISITED BY THE MAJOR INSECT POLLINATOR GROUPS IN PHRYGANA[a]

	Number of			Sucrose/hexose ratio: S/(G + F)	
Pollinator group	Pollinator species	Plant species visited	p–p interactions	Average value on the basis of p–p interactions	SE
Aculeata	49	29	112	2.85	0.532
Apoidea	224	69 (70)	859 (861)	2.58 (2.86)	0.133 (0.236)
Coleoptera	60	46 (47)	248 (249)	1.28 (1.77)	0.178 (0.515)
Diptera (-Syrphidae)	119	53	288	1.06	0.130
Lepidoptera	30	41 (42)	153 (156)	1.69 (4.00)	0.233 (1.344)
Other	48	27	83	1.43	0.395
Syrphidae	46	39	181	0.66	0.108
All community	576	96 (97)	1924 (1930)	1.90 (2.27)	0.080 (0.172)

Numbers in parentheses are with the outlier *Anthyllis* wherever this is visited.

[a] The preference is given as average S/(G + F) ratio calculated over all interactions of an insect group with the plants visited within the community.

TABLE 5. SUCROSE/HEXOSE RATIOS OF THE FLORAL NECTARS VISITED BY THE POLLINATOR GROUPS BROKEN DOWN TO FAMILIES IMPORTANT FOR POLLINATION IN PHRYGANA[a]

Pollinator group	Number of			Sucrose/hexose ratio: S/(G + F)	
	Pollinator species	Plant species visited	p–p interactions	Average value on the basis of p–p interactions	SE
Aculeata	50	30	113	2.82	0.528
Andrenidae	38	33	94	1.02	0.239
Anthophoridae	55	46	232	2.42	0.214
Apidae	3	60 (61)	73 (74)	1.88 (3.50)	0.370 (1.661)
Colletidae	11	15	30	2.05	0.846
Halictidae	43	49	187	2.19	0.286
Megachilidae	73	51 (52)	242 (243)	3.94 (4.42)	0.297 (0.568)
Symphyta	7	7	10	1.01	0.787
Other Hymenoptera	16	13	28	1.22	0.638
Bombyliidae	39	40	116	1.68	0.285
Anthomyid flies	55	26	118	0.56	0.085
Syrphidae	46	39	181	0.66	0.108
Other Diptera	25	26	54	0.81	0.211
Coleoptera	60	46 (47)	248 (249)	1.28 (1.77)	0.178 (0.515)
Lepidoptera	30	41 (42)	153 (156)	1.69 (4.00)	0.233 (1.344)
Hemiptera	23	22	43	1.70	0.617
Neuroptera	2	2	2	0.52	0.490
All community	576	96 (97)	1924 (1930)	1.90 (2.27)	0.080 (0.172)

Numbers in parentheses are with the outlier *Anthyllis* wherever this is visited.

[a] The preference is given as average S/(G + F) ratio calculated over all plant–pollinator interactions within the community. The group "anthomyid flies" encompasses the families Anthomyidae, Muscidae, Calliphoridae, Rhinophoridae, Sarcophagidae, Scatophagidae, and Tachinidae.

Syrphidae: $P < 0.001$). Similarly, the Tukey *a posteriori* HSD test showed that Megachilidae was the only insect family that was distinguished by its preference for high sucrose/hexose ratios, contrasting to Syrphidae and "anthomyid flies" preferring low sugar ratios (Tables 5 and 6).

DISCUSSION

The analysis of the phryganic nectars produced no surprises: they contained the most common sugars known for nectars: sucrose, glucose, and fructose (Wykes, 1952; Percival, 1961; Baker and Baker, 1983). Among the remaining minor sugars, none was consistently found within a group or a family of plants, such as

TABLE 6. SUMMARY RESULTS OF THE POLLINATOR RESPONSES TO NECTAR SUCROSE/HEXOSE RATIOS IN PHRYGANA[a]

	P			
	Aculeata	Anthophoridae	Halictidae	Megachilidae
Andrenidae	0.015			< 0.001
Anthophoridae				< 0.001
Apidae				< 0.001
Halictidae				< 0.001
Other Hymenoptera				< 0.006
Bombyliidae				< 0.001
Anthomyid flies	< 0.001	< 0.001	0.004	< 0.001
Syrphidae	< 0.001	< 0.001	0.002	< 0.001
Other Diptera	0.032			< 0.001
Coleoptera	0.007	0.024		< 0.001
Lepidoptera				< 0.001
Hemiptera				< 0.007

[a] *P* (Tukey HSD posthoc test) shows the difference between the sugar ratios of the nectars preferred by either insect groups. *P* of empty cells or not appearing pairs was NS. The outlier *Anthyllis* was not considered in the calculations.

xylose was in the nectars of the South African *Protea* and *Faurea* (Nicolson and Van Wyk, 1998). Sugar profiles of the phryganic species are commonly found in nature, with a sugar composition similar to that of most other plants.

When focusing on the two plant groups distinguished by their sucrose content and sucrose/hexose ratios (Table 3), the number of species in "high sucrose" (sucrose-dominant to sucrose-rich, according to the terminology by Baker and Baker, 1983) families exceed those of "low sucrose" (hexose-dominant to hexose-rich) families (59% vs. 41%). Although "high sucrose" species make up only 53.5% of the plant species in the community, it is interesting that most of the species flowering in spring–summer had "high sucrose" vs. "high hexose" nectars (60.8% vs. 39.2%, respectively), whereas the opposite holds for winter (36.4% vs. 63.6% for "high sucrose" and "high hexose," respectively). These differences suggest that under the hot and dry Mediterranean conditions "high sucrose" nectars may be selected against "high hexose" ones. Three explanations seem likely. (1) Hexoses, mostly products of postsecretory phenomena of sucrose hydrolysis, may result in osmotic uptake of water throughout anthesis in order to decrease nectar concentration (% w/w) (Pate et al., 1985; Nicolson, 2002). Therefore, nectars rich in hexoses need more water than nectars rich in sucrose for the same amount (weight) of sugars contained (Nicolson, 1998). This may result in water loss for nectars rich in hexoses, and although nectar volumes in the Mediterranean are generally small, the total mount of water loss per plant bearing hundreds of ephemeral, and

generally open, flowers may be appreciable. Under the extreme water limitations characterizing Mediterranean systems, hexose-rich nectar could be an inappropriate solution. (2) From the calorific point of view, nectar with a high sucrose ratio utilizes less water for the same carbohydrate bait offered to pollinators as reward, therefore contributing to water economy in the system (Nicolson, 2002). What is important for honeybees is calorific value of the reward, not the type of sugars (mono-, disaccharides) in nectars of equal calorific value (Wells et al., 1992). (3) The prevalence of "high hexose" nectars in the "winter" flowering species may be related to adaptation of the insect diet to multiple sugar types. Among the nectar sugars dealt with, only sucrose needs digestion (hydrolysis), whereas monosaccharides and water are rapidly absorbed across the midgut (Nicolson, 1998). It may not be by mere coincidence that insects such as syrphids, anthomyid a.o. flies, and beetles find monosaccharide uptake easier compared to sucrose as a quick drink or as a normal meal (Table 6). Hence, adaptation to easy-to-digest monosaccharides may constitute a differential advantage of hexose-nectars for attracting an extensive array of pollinators, which to a large extent are nonspecialized and most of which are active in wintertime.

Deep flowers have been associated mostly with pollination by specialized pollinators and protection from nectar thieves, enabling the preservation of nectar *quantity* (Baker and Baker, 1983, 1990). What has been underestimated so far is the protection of nectar *quality*, which can result by either open contact with air (evaporation, oxidation) or with a continuous contact with many non-legitimate yeast- or bacteria-bringing insects (fermentation). I argue that deep flowers are the most convenient places for nectars to be preserved. Unless protected, nectar tends to equilibrate with ambient humidity, its concentration being determined by both chemical effects and microclimatic gradients (Corbet et al., 1979; Nicolson, 1998, 2002). On the other hand, deep and closed flowers are efficient in protecting the nectar so that unwanted insects have limited access. In this respect, numerous hairs and stamens are as important as long corollas in restricting air movement and excluding insects, such as *Cistus parviflorus*, *C. salvifolius*, and *Capparis spinosa*, all key species in phrygana, comparable to the South African Proteaceae (Petanidou and Ellis, 1996; Nicolson, 2002). The presence of honey leaves or honey pockets (i.e., petal scales where nectar is accumulated) in bowl-shaped flowers in some phrygana species, probably plays a similar nectar-protective role (e.g., *Nigella arvensis*, *Ranunculus sprunerianus*).

As shown, "high sucrose" nectars prevail in deep flowers vs. "high hexose" nectars that are frequent in open flowers. Thus, plants bearing deep flowers with "high sucrose" nectars are most successful during the difficult period of the year, i.e., between April and mid-September when evapotranspiration exceeds rainfall (Petanidou and Ellis, 1993), allowing open or bowl-shaped "high hexose" flowers to thrive in fall through winter. Yet, this seasonal shift in

flowering time may constitute a potential trade-off for many, albeit unspecialized and illegitimate flower visitors (Petanidou et al., 1995).

Phylogenetic Constraints. That sucrose/hexose ratios were associated with plant family membership in the phrygana community studied was not a surprising result. This confirms previous conclusions by Percival (1961), Baker and Baker (1983), and Stiles and Freeman (1993) that the primary constraints responsible for shaping sugar profiles in the floral nectars of plants are phylogenetic. This is interesting, bearing in mind that Mediterranean communities may differ greatly from other continental communities in this respect. For instance, phylogenetic constraints were not found to play a decisive role in determining plant flowering time in phrygana, as seen elsewhere (Kochmer and Handel, 1986; Petanidou et al., 1995).

Lamiaceae, a key family of the phrygana, is also the top sucrose rewarding plant family in this community (Petanidou and Vokou, 1993; Petanidou, 1996; Petanidou and Ellis, 1996; Petanidou et al., 2000). Interestingly, in all earlier studies, Lamiaceae have been pinpointed for their high rate of sucrose-dominant to sucrose-rich nectars (Percival, 1961; Baker and Baker, 1983), although only in phrygana do all Lamiaceae species have "high sucrose" nectars. This high rate can be explained as an effect of other overwhelming constraints in the Mediterranean, such as climate or a diverse bee fauna (Michener, 1979). With high values in sucrose content, Ranunculaceae follows the Lamiaceae, probably due to its small plant number (3) and the ultra conservative *posthoc* test applied. These findings agree with Baker and Baker (1983), who found sucrose-dominant or sucrose-rich nectars in Ranunculaceae, but not with Percival (1961). Finally, Fabaceae, with very high sucrose values (Table 3) occupies an inferior position, also probably due to the heterogeneity within this group, as confirmed by Percival (1961) and Stiles and Freeman (1993). Apiaceae and Liliaceae, the "low sucrose" families of the community, lie on the opposite side of the scale as found by Percival (1961) and Baker and Baker (1983). It should be noted that all the above families are reasonably phylogenetically independent, being placed far apart in the evolutionary tree (Dodd et al., 1999), which makes convergence/divergence in their sugar ratios meaningful. The results allow for the conclusion that phryganic nectars are, to a large extent, shaped by phylogenetic constraints as found in earlier studies.

Ecological Constraints. That nectar composition (as sucrose/hexose ratio and % sucrose content) is not associated with the plant life cycle, a character resulting from complex ecological factors, is surprising. This, together with the finding that the sugar ratio does not depend on flowering time, may lead one to the conclusion that ecological constraints do not appear to have a detectable effect in shaping nectar composition in the Mediterranean communities. However, when the period of actual water deficit in the system (April–mid-September) is considered, it emerges that plants flowering in the dry period do

differentiate significantly in nectar composition from those flowering in the wet period. This result is notable because it underlines the importance of time, as an expression of water availability within the system, in effectively shaping many pollination-related attributes found in other studies, such as flowering (Petanidou et al., 1995), corolla size of flowers, as well as some nectar and nectary attributes (Petanidou et al., 2000). This study confirms that time constitutes a critical parameter in the Mediterranean, because of the overriding effect of the summer drought that characterizes these communities.

Coevolutionary Constraints. The results also provide evidence of a significant partitioning of nectar resources by the existing pollinator guilds within the community, based on the sugar profiles of the nectars. This confirms Baker and Baker (1983, 1990), but their results were derived from "pollination syndromes" and predominant pollinators alone. My results, in contrast, are based on all plant–pollinator interactions observed in the entire community throughout the year, and they consider not only predominance, but also statistical variation.

The highest preference for nectars of high sucrose content in the phrygana is shown by wasps (aculeates) and bees. The differential preference of bees for visiting flowers with high-sucrose nectars is not only in contrast to beetles, hoverflies, and other flies (as is also the case for wasps), but also includes butterflies, a heterogeneous group (Tables 4 and 5). In this respect, my conclusions do not support those of Baker and Baker (1983) that butterflies prefer sucrose-dominant to sucrose-rich nectars as long-tongue bees do. On the other hand, my data show that bees are a heterogeneous group too, with nectar preferences varying from low- and medium-sucrose (e.g., Andrenidae; Apidae, Halictidae, and Anthophoridae) to high sucrose (Megachilidae; cf. Table 6). The tendency of Megachilidae to exploit such high-sucrose nectars is certainly related to their long-tongue morphology allowing them to obtain nectar from deep flowers. Like bees, wasps are the only group in the community showing a differential preference (vs. beetles, hoverflies a.o. flies, as well as Andrenidae) to visit flowers with "high sucrose" nectars (Tables 4–6). This finding shows that wasps are important as reward consumers and probably as pollinators in these semiarid environments.

Megachilidae are the only group showing a high preference for sucrose-nectars. This family is diverse within the Mediterranean Basin (Michener, 1979), by far the most species-rich in phrygana [32% of the bees and 13% of the anthophilous insect fauna according to Petanidou and Ellis (1993)], and a key family in Mediterranean communities (Petanidou and Ellis, 1996; Petanidou et al., unpublished data). Although little is known of the nectar sugar preferences of solitary bees, experiments on social bees and other animals have shown significant preference differences: honeybees showed no preference for either sugar type of equal calorific value (1 M sucrose vs. 2 M monosaccharides; Wells et al., 1992), but *Melipona beecheii* and *M. fasciata* preferred sucrose to

glucose and fructose (Biesmeijer et al., 1999). Similarly, the peacock butterfly, *Inachis io*, strongly prefered sucrose over fructose, especially over glucose (Rusterholz and Erhardt, 1997). Bearing in mind that sucrose-nectars are advantageous to plant–pollinator relationships in phrygana (see above), I argue that the high rate of sucrose-nectars in the phryganic communities may constitute an ecophysiological response to water constraints, and could be the main driver for floral preferences by their pollinator mutualists. By being the most numerous and representative group in phrygana, the long-tongue Megachilidae can respond to the conditions set above (sucrose-nectars in deep flowers), hence they probably represent the main selecting pollinator group for "high sucrose" nectars in the Mediterranean region.

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