Plant Syst. Evol. 238: 69–86 (2003)
DOI 10.1007/s00606-002-0269-y

Plant Systematics and Evolution
Printed in Austria

Nectar sugar composition in angiosperms from Chaco and Patagonia (Argentina): an animal visitor's matter?

L. Galetto and **G. Bernardello**

Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC), Córdoba, Argentina

Received August 27, 2002; accepted December 17, 2002

Abstract. We relate nectar sugar composition with floral visitors in samples from two biogeographic regions from Argentina: Chaco (99 spp. from its southern region) and Patagonia (48 spp. from its central region), using our own data published in earlier papers. The variables to be compared were sugar ratio and sucrose percentage. Differences in the sugar composition were observed when comparing both regions. Bee- and butterfly-visited Patagonian species showed lower sucrose percentages and sugar ratios than Chaquean species; i.e., a convergence in sugar composition was not verified. Moth-visited species showed a wide range of sucrose proportions and sugar ratios in both regions with no significant differences between them. As the differences found in sugar ratio between Chaco and Patagonia, according to the predominant pollinator guilds, may have been influenced by the sample size, we searched for similarities in sugar ratios between plants with the same visitor type in a comparative way, comparing our data pooled together against data by Baker and Baker's (1983a). Our data do not agree with theirs, i.e., no trends can be drawn for bees, moths, and butterflies sugar preferences. The exceptions were the hummingbird-visited species that showed a similar pattern in both cases, i.e., there is a convergence among plants offering nectar with a predominance of sucrose. To evaluate whether closely related species within a family have similar nectar composition and flower visitors, regardless of their region, sugar proportions were compared in several families. Hexose nectars were predominant in Asteraceae, Fabaceae, Solanaceae, and Verbenaceae, while sucrose nectars prevailed in Bromeliaceae and Onagraceae. Nectar composition seems to be a more conservative trait than flower morphology. This may be a reason to explain the absence of a convergence in sugar composition between plants growing in different biogeographical regions that share the same animal visitor guilds.

Key words: Angiosperms, nectar sugar composition, pollination, hummingbirds, bees, moths, butterflies, convergence, phylogenetic constraints, Chaco, Patagonia, Argentina.

Nectar is the most common mean by which animal-pollinated plants reward their pollen vectors (Proctor et al. 1996). Thus, the nectariferous plants of a given area are an important energy resource for visitors (Kevan and Baker 1999). Baker and Baker (1983a) recommended to study of nectar chemistry and pollination biology on an ecosystem basis, rather than just taking flower and visitor species in isolation, because the pollinators in a given area may be a reflection of the aggregate floral rewards offered.

Sugars dominate the total nectar solutes and represent the major energy source for visitors (e.g. Percival 1961; Baker and Baker

1983a, b; Stiles and Freeman 1993). Other substances, e.g. amino acids, antioxidants, lipids, phenols, etc., are found as well, mostly in trace quantities (Baker and Baker 1975, 1983b). All its components often convey a specific taste and/or odour that may be important for maintaining pollinators. On the other hand, success in attracting pollinators is a relative matter. The presence of other flowers with more desirable nectar in the vicinity will result in the neglect of the less desirable ones, but at the same time, the "absence of highly attractive competitors may mean that only partially desirable nectar will be taken by 'desperate' visitors" (Baker and Baker 1983a).

Nectar sugars may occasionally vary within a species (e.g. Bernardello et al. 2000), but sugar proportions are comparatively stable for most species. These sugars are mainly the disaccharide sucrose and the hexose monosaccharides fructose and glucose varying from an almost pure solution to a differently balanced combination (e.g. Percival 1961; Baker and Baker 1975, 1983a, b).

In general, sugar composition varies among species and has been related either to the pollinator guild or to the flower syndrome of the plant species. There is a tendency in the literature, chiefly following Baker and Baker (1975; 1983a, b; 1990), to associate nectar sugar composition to the visitor guilds, i.e. every kind of anthophilous animal would prefer certain components or certain combination, which suggests the existence of a co-evolution between them. Baker and Baker based these trends on their own, mostly unpublished data on nectar chemical composition from North and Central American plants. Pollinators have the choice to select the species they visit when faced to a diverse array of flowers with varied nectar sugar proportions. Differences among pollinator's preferences have been explained on the basis of the specific taste and odour that different sugars convey to nectar (Pham-Delegue et al. 1990), of the enzymatic capability of floral visitors related to the efficiency of sucrose absorption (Martínez del Río et al. 1988, Downs and Perrin 1996), and of different sugar compositions needed to fulfil nutritional and energetic animal requirements (Southwick et al. 1981).

In some plant groups, a positive pollinator-adaptation was reported in determining the nectar sugar components (e.g. Baker and Baker 1983a, Dafni et al. 1988), but in other groups, the available data indicate that sugar composition is a conservative character that reflects phylogenetic constraints (van Wyck et al. 1993, Galetto et al. 1998, Perret et al. 2001). Baker and Baker (1983a) were particularly conscious of this problem when they wrote (p. 131): "Many of the long-tongued bee flowers in our sample come from the Lamiaceae and Ranunculaceae, families characterized by sucrose-richness is common, as well as from the genera of the Scrophulariaceae in which sucrose-richness is common. By contrast, many of the short-tongued bee-flowers are members of the Brassicaceae and Asteraceae which have the opposite characterization. It is difficult to see how one can resolve which is the cart and which is the horse in these relationships".

To give an insight into this matter, we here made a quantitative attempt to answer if convergence occurs in the nectar sugar composition of plant species visited by the same kind of pollinator guilds in samples from two biogeographical regions of Argentina. If flower visitors are modelling sugar composition according to their preferences, we would expect to find similar tendencies within guilds when comparing species from these regions. Nevertheless, caution must be taken when interpreting nectar characteristics strictly in terms of pollinator selection. Several authors have pointed out that members of a single clade can be expected to have the same floral trait because they share recent ancestors, rather than because they share some ecological features (Armbruster 1996, Silvertown and Dodd 1997). Thus, we also examined sugar composition within families in order to analyse phylogenetic relatedness.

We used two data sets on Patagonian and on Chaquean plants, taken from our previously published works. The Patagonia is a semi desert shrubland and its climate is dry and cold with strong winds, snowfalls in winter, and frosts almost all the year round (Cabrera 1971); we studied Patagonian plants from the southern region, known as "chubutense district" (mean annual temperature 12–14 °C, mean annual rainfall 200 mm). The Chaco is a vast region covering plains of Argentina, Paraguay, Bolivia and Brazil, mainly covered with semiarid forests and woodlands with continental climate (moderate to scarce rains, mild winters and hot summers; Cabrera 1971); we analysed Chaquean plants mostly from the "Chaqueño Serrano district" (mean annual temperature 20–22 °C, mean annual rainfall 800 mm). The studied regions are over 1,200 km apart.

Material and methods

Data on a total of 147 studied species from both regions were taken from previous papers (see Appendix 1 for Chaco: 99 species, and Appendix 2 for Patagonia: 48 species), in which provenance, sample size, collectors, etc., can be found. Sugar analysis was done in all cases using gas–liquid chromatography, following Sweeley et al. (1963) as explained in Forcone et al. (1997). The main floral visitors were determined by using our own field data, most of them published in the cited papers, but complemented by new unpublished observations.

Statistical analyses were performed using methods described in Sokal and Rohlf (1995). Kruskal-Wallis one-way analysis of variance was used to compare sucrose percentage and sugar ratio between species from Chaco and Patagonia grouped by visitor type, because data distributions depart from normality (Kolmogorov-Smirnov test for goodness of fit). The statistical program package SPSS (1992) was used for all analyses.

Frequencies of the species with the same visitor guild (VG: moth, bees, and butterflies) and biogeographical region (BR: Chaco and Patagonia) were compared by a VG x BR contingency table. Our data pooled from both studied regions were compared with those published by Baker and Baker (1983a) for the different pollinator groups; frequencies of different sugar ratios (SR: sucrose dominant, sucrose rich, hexose rich, and hexose dominant) and data sets (DS: Argentina, Baker and Baker's) were compared by a SR x DS contingency table. The differences found in sugar ratio between Chaco and Patagonia, according to the predominant floral visitors, may have been influenced by the sample size. As Baker and Baker (1983a) published a data set based on a larger sample of plant species from a wide range of habitats and climatic zones, we searched for similarities in sugar ratios between plants with the same visitor type, comparing our data pooled together against theirs (Baker and Baker 1983a: Tables 5–10). For a conservative comparison, we combined bee and moth categories from Baker and Baker (1983a). Finally, it is necessary to point out that there is no overlapping between our data and Baker and Baker's (1983a).

To evaluate if closely related species within a family have similar nectar composition, irrespective of the biogeographical region (Chaco and Patagonia) where they grow, we compared sugar proportions in seven families in which at least ten species have been examined.

Results

First of all, we assessed if the sampled species from the Chaquean and Patagonian regions were comparable in terms of number of species visited by the different animal visitor guilds. Significant differences were found between them ($\chi^2_{[3,\ 140]} = 17.9$; $P < 0.0001$), when comparing all the guilds with more than five species in each region (Fig. 1). As hummingbird-visited species are absent in Patagonia, this guild was removed from the analysis, and the frequencies for bee-, moth-, and butterfly-visited species were analogous between Chaco and Patagonia ($\chi^2_{[2,\ 116]} = 3.02$; $P = 0.22$). Thus, we only used these three animal guilds to evaluate if there is a convergence in the nectar sugar composition of plant species at a biogeographical scale.

Nectar sugar composition. Differences in the sugar composition were observed when comparing Chaco and Patagonia ($H = 8.9$, $P = 0.01$; $H = 9.02$, $P = 0.01$, for sucrose percentage and sugar ratio, respectively; Figs. 2,

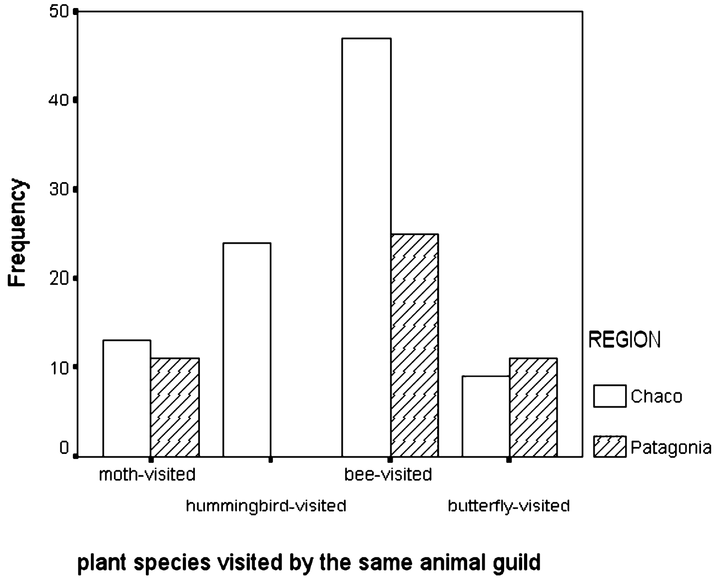

Fig. 1. Frequency histogram showing the number of species for each animal visitor's guild in Chaco and Patagonia

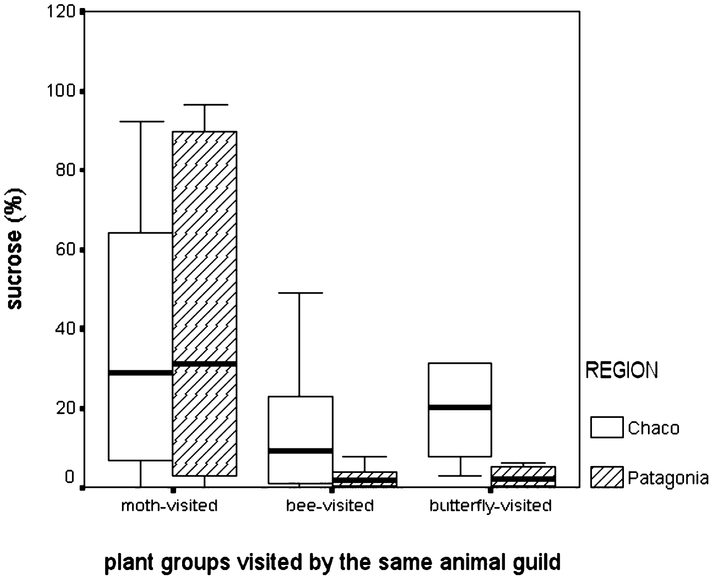

Fig. 2. Box-plot of the percentage of sucrose for each plant group with the same animal visitor guild in Chaco and Patagonia. *A posteriori* analyses showed that the differences were significant between regions for flowers visited by bees and butterflies but not for flowers visited by moths

3). Bee- and butterfly-visited Patagonian species showed lower sucrose percentages (Fig. 2) and sugar ratios (Fig. 3) than Chaquean species. In other words, a convergence in sugar composition was not observed. On the other hand, moth-visited species showed a wide range of sucrose proportions (Fig. 2) and sugar ratios (Fig. 3) in both regions, with no significant differences between them.

Sugar ratios and pollinator guilds. In general, our data do not agree with Baker and Baker (1983a; Table 1) and no trends can be drawn for bees', moths', and butterflies' sugar preferences. The only exception are hummingbird-visited species that showed a similar pattern for the different categories of sugar ratios of the whole data set, i.e. there is a clear convergence among hummingbird-visited

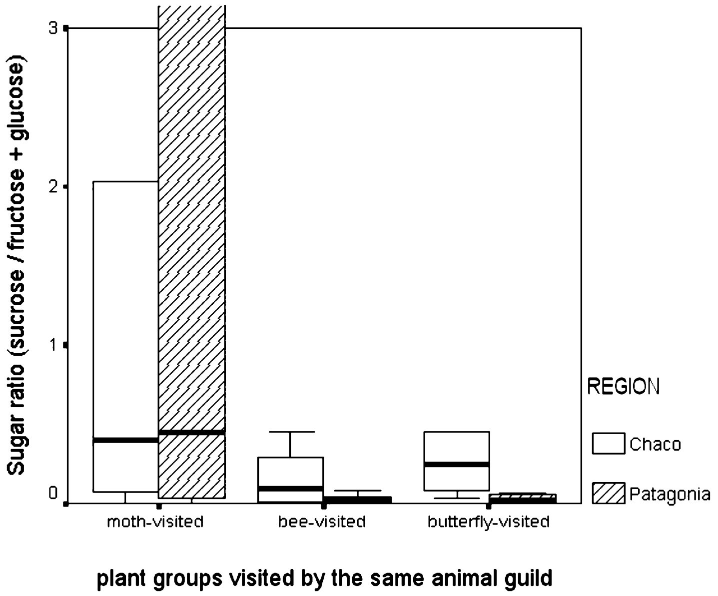

Fig. 3. Box-plot of the sugar ratio for each plant group with the same animal visitor guild in Chaco and Patagonia. *A posteriori* analyses showed that the differences were significant between regions for flowers visited by bees and butterflies but not for flowers visited by moths

Table 1. Comparison of sugar ratios according to the visitor type from Baker and Baker (1983a) and our data. Data are: frequency in number of species (relative percentage within the visitor type category for each data set). χ^2 stands for the frequencies

Nectar sugar ratio	Data	Moth-visited species	Bee-visited species	Butterfly-visited species	Hummingbird-visited species
Hexose dominant	Present work	8 (33.3)	45 (62.5)	12 (60.0)	0 (0)
	Baker and Baker	5 (4.8)	128 (27.5)	5 (6.6)	0 (0)
Hexose rich	Present work	5 (20.8)	18 (25.0)	5 (25.0)	3 (12.5)
	Baker and Baker	22 (21.1)	178 (38.2)	17 (22.6)	18 (12.8)
Sucrose rich	Present work	2 (8.3)	2 (2.7)	1 (5.0)	7 (29.5)
	Baker and Baker	30 (28.8)	77 (16.5)	24 (32.0)	45 (32.1)
Sucrose dominant	Present work	9 (37.5)	7 (9.7)	2 (10.0)	14 (58.3)
	Baker and Baker	47 (45.2)	83 (17.8)	29 (38.7)	77 (55.0)
Statistical test		$\chi^2_{[3,\ 126]} = 18.8$ $P < 0.0001$	$\chi^2_{[3,\ 537]} = 22.1$ $P < 0.0001$	$\chi^2_{[3,\ 96]} = 33.9$ $P < 0.0001$	$\chi^2_{[3,\ 163]} = 0.08$ $P = 0.96$

plants offering nectar with a predominance of sucrose.

Phylogenetic constraints. We evaluate if closely related species within a family have similar nectar composition, regardless of the biogeographical region, comparing sugar proportions in several families. Most of them (Asteraceae, Fabaceae, Solanaceae, Verbenaceae) showed a tendency to have hexose nectars (either dominant or rich), while two (Bromeliaceae, Onagraceae) predominantly sucrose nectars (Fig. 4). On the other hand, Bignoniaceae showed about the same number of species with sucrose or hexose predominant nectars (Fig. 4).

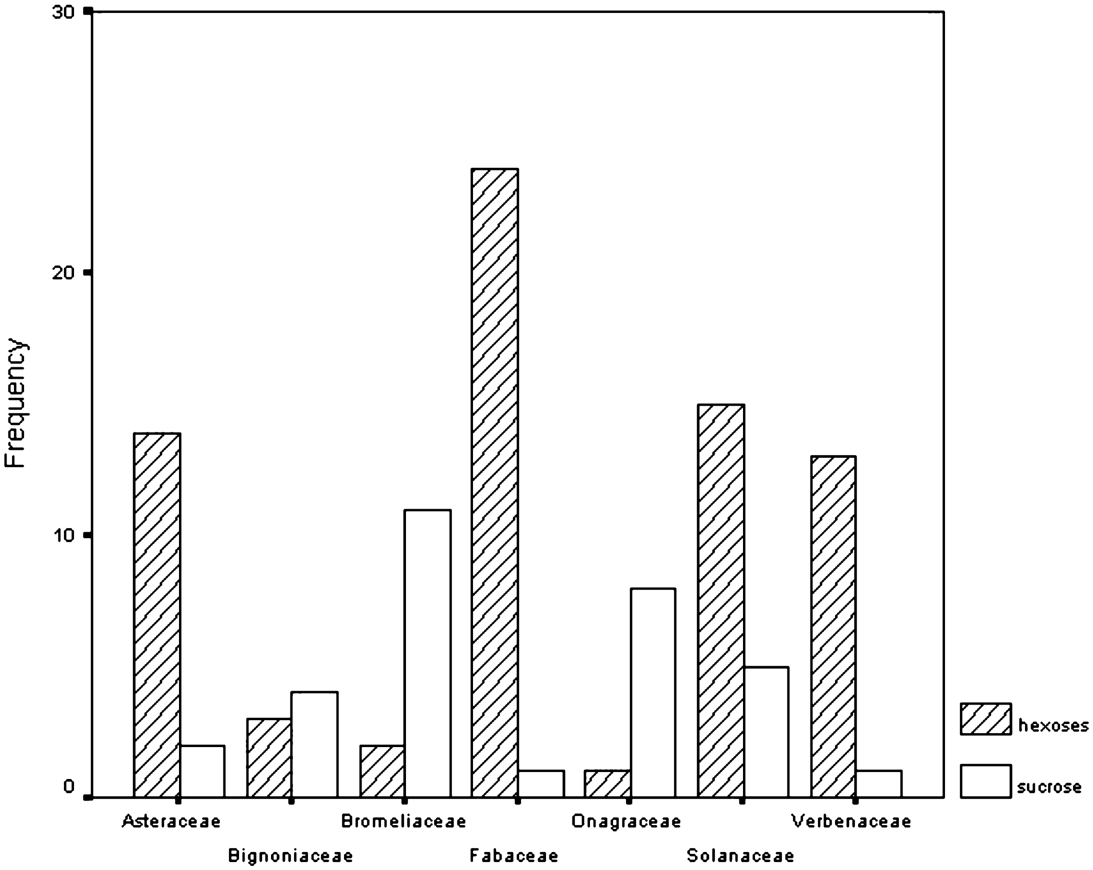

Fig. 4. Frequency histogram showing number of species with hexose or sucrose predominant nectar in seven compared families that inhabit Chaco and Patagonia

Discussion

Baker and Baker (1983a, 1990) indicated that nectar sugar ratios show a close relationship with the pollinator type that visit the flowers, irrespective of the plants taxonomic order. Thus, when nectar composition is taken in conjunction with the flower and inflorescence morphology, sugar ratio can be a good predictor of the pollinators a plant species may have (Baker and Baker 1983a).

Our data on sugar composition did not match with the preferences suggested by Baker and Baker (1983a, b) for the different animal groups that visit flowers, with the exception of the nectar type of the hummingbird-visited plants in the Chaco. Effectively, hummingbird flowers tended to produce a sucrose-dominant nectar in North, Central and South America (e.g. Baker and Baker 1983a; Freeman et al. 1984, 1985; Gottsberger et al. 1984; Stiles and Freeman 1993; Baker et al. 1998). In addition, experimental studies on sugar preferences of these birds showed that they preferred sucrose solutions instead of equivalent monosaccharides ones (e.g. Martínez del Río 1990, Stromberg and Johnsen 1990). Hummingbirds are very well known for taking nectar on a large scale and for being limited to the New World (Proctor et al. 1996). It is thought that hummingbird lineages began to radiate early in the Miocene, diversifying from South to North America (Bleiweiss 1998). The relationship between floral nectar and hummingbird's sugar preferences is consistent in all the distribution range of these birds, even though the hummingbird–plant interactions are recent in the evolutionary time compared to the time of radiation of the insect orders that assiduously visit flowers.

Although more ecosystem based data are needed, the available studies in the American continent suggest that nectar characteristics not always tend to be similar for plants visited by the same animal taxa as it was formerly thought. The limitations may be in what the plants can produce in a certain climate, in that certain areas have not hummingbird–plant interactions, or simply due to phylogenetic constraints. For instance, the studied Patagonian plants (Forcone et al. 1997, Bernardello et al. 1999), as well as plants from the Alpine zone in the Colorado Rockies (Baker and Baker 1983a), showed hexose dominance in general. These regions have severe climatic conditions and absence of hummingbird-visited species. On the contrary, data on regions from the U.S.A. (Freeman and Worthington 1985), Mexico (Freeman et al. 1985), Brazil (Gottsberger et al. 1984), and the Argentinean Chaco (lit. cited in Appendix 1) showed many species with sucrose-dominated nectars, where the climate is moderate and there are many hummingbird-visited species.

Several authors have pointed out that taxonomically related plants showed the same pattern in nectar sugar because they share common ancestors, rather than because they share the same floral visitors. Since the data published by Percival (1961), many authors have recognized trends in sugar composition within certain families (e.g. Baker and Baker 1983a), tribes (Elisens and Freeman 1988, Perret et al. 2001, Torres and Galetto 2002), and genera (van Wyk 1993, van Wyk et al. 1993, Galetto et al. 1998) independently of their visitors. As an example, nectar sugar composition was documented for 45 species of tribe Sinningieae (Gesneriaceae), which exhibit hummingbird, bee, bat, and moth syndromes (Perret et al. 2001); nevertheless, the nectar of all but one species is sucrose-dominated, indicating that nectar chemistry is conservative within this monophyletic plant group (Perret et al. 2001). Phylogenetic constraints seem to be also influencing nectar sugar composition. Thus, nectar composition is a trait more conservative than flower morphology (e.g. van Wyk et al. 1993, Galetto et al. 1998, Perret et al. 2001), which suggests that the plant–visitors interactions may determine rapid changes in flower structure (Galen 1996) in comparison to changes in nectar composition. This may be a reason to explain the absence of a convergence in sugar composition between plants growing in different biogeographical regions that share the same animal visitor guilds. A question remains open: does the convergence in sugar composition between hummingbird-visited plants growing in different regions mainly respond to the animal–plant interaction, or to the taxonomic membership of the plants?

We thank the institutions which have supported our research for the last 10 years: CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Secretaría de Investigaciones Científicas y Técnicas de la Universidad Nacional de Córdoba, CONICOR (Consejo Investigaciones Científicas y Técnicas de la Provincia de Córdoba), Agencia Córdoba Ciencia, Agencia Nacional de Promoción Científica y Técnica, and National Geographic Society. Héctor Juliani and Norma Perassi provided lab facilities. Alicia Forcone and Carolina Torres provided personal observations on floral visitor's on some Patagonian plants and on Chaquean Asteraceae, respectively.

Appendix 1. Analysed species from the Argentinean Chaco region, indicating nectar sugar ratio (sucrose/fructose + glucose), percentages of sucrose, fructose, and glucose in nectar, floral visitors, and literature from where data were taken

Family	Taxon	Sugar ratio	% sucrose	% fructose	% glucose	Main floral visitors	Other floral visitors	# of visitors' Orders	Literature
Apocynaceae	*Macrosiphonia petraea* (A. St. Hil.) K. Schum.	5.6	84.9	3.7	11.3	moths		1	Galetto 1997
	Mandevilla laxa (Ruiz & Pav.) Woodson	5.9	85.5	8.3	6.1	hummingbirds	bees	2	Galetto 1997
	M. pentlandiana (A. DC.) Woodson	2	66.7	18	15.2	bees	hummingbirds	2	Galetto 1997
Asclepiadaceae	*Amblyopetalum coccineum* (Griseb.) Malme	0.6	31.5	28.8	39.5	butterflies		1	Morales 1999
	Morrenia brachystephana Griseb.	4.4	79.8	17.3	2.9	wasps	bees, butterflies	3	Galetto 1993
	Oxypetalum arnottianum Buek	1	48.9	23.6	27.5	flies		1	Morales 1999
	Philibertia gilliesii Hook. & Arn.	0.03	3.1	66.3	30.7	flies	wasps, bees, beetles	4	Galetto 1993
Asteraceae	*Eupatorium hookerianum* Griseb.	0.09	8	40.9	50	butterflies	bees	2	Torres and Galetto 2002
	Flourensia campestris Griseb.	0.08	8	40.7	51.1	bees	flies, butterflies, beetles, wasps	5	Torres and Galetto 2002
	Gaillardia megapotamica (Spreng.) Baker	0	0	39.1	60.8	bees	flies, butterflies, beetles	4	Torres and Galetto 2002
	Grindelia discoidea Hook. & Arn.	0.01	1.2	38.8	60	bees	butterflies, beetles	3	Torres and Galetto 2002
	Helenium argentinum Ariza	0.01	0.6	42.3	57.1	bees	flies, butterflies, beetles	4	Torres and Galetto 2002
	Hyaloseris rubicunda Griseb.	0.9	48.2	19.6	32.1	hummingbirds		1	Galetto 1995a
	Hypochoeris radicata L.	0.05	4.5	35.3	60.2	bees	flies	2	Torres and Galetto 2002
	Mikania urticifolia Hook. & Arn.	0.1	9.4	47	43.6	bees	flies, beetles, butterflies	4	Torres and Galetto 2002
	Solidago chilensis Meyen	0.2	18.1	36.8	45.1	bees	beetles, flies, butterflies	4	Torres and Galetto 2002

Appendix 1 (continued)

	Stevia satureifolia (Lam.) Schultz Bip.	0.04	3.8	42.2	54	butterflies	bees, flies	3	Torres and Galetto 2002
	Trichocline reptans (Wedd.) Rob.	0.01	1.1	43.9	55	bees	flies, butterflies	3	Torres and Galetto 2002
	Trixis divaricata (Kunth) Spreng.	0.3	23.2	32.7	44.1	bees	flies	2	Torres and Galetto 2002
	Vernonia mollisima Hook. & Arn.	0.3	21.5	31.8	46.6	bees	butterflies	2	Torres and Galetto 2002
	Zexmenia buphtalmiflora (Lorentz) Ariza	0.04	4.2	46.6	49.1	bees	flies, butterflies, beetles	4	Torres and Galetto 2002
	Zinnia peruviana (L.) L.	9.4	90.3	2.3	7.3	butterflies	bees	2	Torres and Galetto 2002
Bignoniaceae	*Arrabidaea truncata* (Sprague) Sandwith	0.14	11.9	48.8	39.2	bees		1	Galetto 1995b
	Dolichandra cynanchoides Cham.	1.1	51.9	19.4	28.6	hummingbirds	bees	2	Galetto 1995b
	Macfadyena dentata K. Schum.	1.6	60.8	22.9	16.2	bees		1	Galetto 1995b
	M. unguis-cati (L.) A. H. Gentry	0.2	19.2	25	55.7	bees		1	Galetto 1995b
	Pithecoctenium cynanchoides Cham.	1.5	60.9	16.8	22.2	bees	beetles	2	Galetto 1995b
	Tecoma garrocha Hieron.	0.8	45.4	20.6	33.9	hummingbirds	bees	2	Galetto 1995b
	T. stans Kunth	0.03	3	39.6	57.3	bees		1	Galetto 1995b
Bromeliaceae	*Bromelia serra* Griseb.	0.2	15.7	51.3	32.9	hummingbirds		1	Bernardello et al. 1991
	Deuterocohnia brevifolia (Griseb.) M. A. Spencer et L. B. Sm.	5.1	84.4	5.3	10.3	hummingbirds		1	Bernardello et al. 1991
	D. longipetala (Baker) Mez	0.8	46.4	23.9	29.7	hummingbirds		1	Bernardello et al. 1991
	D. schreiteri A. Cast.	2	66.7	9.1	24.1	hummingbirds		1	Bernardello et al. 1991
	Dyckia aff. gilliesii Baker	0.5	34.9	24	41	hummingbirds		1	Bernardello et al. 1991
	D. floribunda Griseb.	1	49.4	19.4	31.2	hummingbirds	butterflies, bees, moths	4	Bernardello et al. 1991

Appendix 1 (continued)

Family	Taxon	Sugar ratio	% sucrose	% fructose	% glucose	Main floral visitors	Other floral visitors	# of visitors' Orders	Literature
	D. ragonesei A. Cast.	1.7	63.1	11.6	25.3	hummingbirds		1	Bernardello et al. 1991
	D. velazcana Mez	0.3	29.7	29.3	41	hummingbirds	butterflies, bees	3	Bernardello et al. 1991
	Puya spathacea (Griseb.) Mez	1	50.2	23.8	25.9	hummingbirds	bees	2	Bernardello et al. 1991
	Tillandsia duratii Vis.	5.1	83.4	4.2	12.2	hummingbirds		1	Bernardello et al. 1991
	T. ixiodes Griseb.	4.1	80.2	5.1	14.6	hummingbirds		1	Bernardello et al. 1991
	T. lorentziana Griseb.	6	85.7	4.2	10	hummingbirds		1	Bernardello et al. 1991
	T. xiphioides Ker Gawl.	10	95.4	1.5	3.1	hummingbirds		1	Bernardello et al. 1991
Buddlejaceae	*Buddleja mendozensis* Benth.	0.14	10.8	67.9	21.3	bees	butterflies, flies	3	Galetto 1993
Cactaceae	*Opuntia cordobensis* Speg.	0.01	1	39.4	59.5	bees	beetles	2	Morales 1999
	Trichocereus candicans (Salm-Dyck) Britton & Rose	0.3	22.6	34	43.4	bees	beetles	2	Morales 1999
Campanulaceae	*Siphocampylus argentinus* E. Wimm	2.9	74.1	19.6	6.2	hummingbirds		1	Galetto et al. 1993
	S. foliosus Griseb.	6.5	86.6	11.2	2.1	hummingbirds		1	Galetto et al. 1993
	S. nemoralis Griseb.	5.5	84.5	12.1	3.3	hummingbirds		1	Galetto et al. 1993
Cucurbitaceae	*Cucurbita maxima* ssp. *andreana* (Naudin) Filov	2.03	67	13	20	bees	butterflies, beetles, flies	4	Ashworth and Galetto 2001
Euphorbiaceae	*Croton sarcopetalus* Müll. Arg.	0	0	30	70	bees	wasps, flies, beetles, butterflies	4	Freitas et al. 2001

Appendix 1 (continued)

Fabaceae	*Caesalpinia coluteifolia* Griseb.	0.01	1.1	24.6	74.3	bees		1	Cocucci et al. 1992
	C. exilifolia Griseb.	0.004	0.4	36.7	62.9	bees		1	Cocucci et al. 1992
	C. gilliesii (Hook.) D. Dietr.	0.1	11.7	34.8	53.5	moths	hummingbirds, bees	3	Cocucci et al. 1992, Jausoro & Galetto 2000
	C. paraguariensis (D. Parodi) Burkart	0.5	31.4	18.3	50.3	bees		1	Cocucci et al. 1992
	Cercidium praecox (Ruiz et Pav.) Burkart & Carter	0.05	7.3	32.7	60	bees		1	Cocucci et al. 1992
	Erythrina crista-galli L.	0.003	0.3	34.9	64.8	bees	hummingbirds, butterflies, flies	4	Galetto et al. 2000
	Geoffroea decorticans (Hook. & Arn.) Burkart	0.3	20.4	33.6	45.8	bees	flies, butterflies	3	Morales 1999
	Hoffmannseggia glauca (Ortega) Eifert	0.2	14.7	27	58.3	bees		1	Cocucci et al. 1992
	Parkinsonia aculeata L.	0.02	2.6	32.9	64.5	bees		1	Cocucci et al. 1992
	Prosopis alba Griseb.	0.2	11.8	43.8	44.4	bees	wasps, flies, beetles, butterflies	5	Morales 1999
Loranthaceae	*Ligaria cuneifolia* (Ruiz & Pav.) Tiegh.	1.3	56.5	15.9	27.5	hummingbirds	bees	2	Galetto et al. 1990
Nyctaginaceae	*Bouganvillea stipitata* Griseb.	0.08	7.2	43.3	49.5	moths		1	López and Galetto 2002
Onagraceae	*Oenothera affinis* Cambess.	0.69	41	26	33	moths	bees	2	Morales 1999
	Oe. indecora Cambess.	9	92.3	6	2	moths	bees	2	Morales 1999
	Oe. rosea Aiton	10	93.2	3	4	butterflies	bees	2	Morales 1999
Orchidaceae	*Beadlea dutraei* (Schltr.) Garay	8.3	89.1	4.5	6.3	bees		1	Galetto et al. 1997
	Habenaria gourlieana Gillies ex Lindl.	7.9	88.9	4.8	6.4	moths		1	Galetto et al. 1997
	H. hieronymi Kranzlin	0.2	16.5	27.4	56.1	bees		1	Galetto et al. 1997

Appendix 1 (continued)

Family	Taxon	Sugar ratio	% sucrose	% fructose	% glucose	Main floral visitors	Other floral visitors	# of visitors' Orders	Literature
	Pelexia bonariensis (Lindl.) Schltr.	1.7	63	13.4	23.6	bees		1	Galetto et al. 1997
	Stenorrhinchos orchioides (Sw.) Rich.	0.5	33.2	29.6	37.2	hummingbirds		1	Galetto et al. 1997
Oxalidaceae	*Oxalis chrysantha* Progel	0.3	24.9	31.9	43.2	bees	beetles, flies	3	Morales 1999
Passifloraceae	*Passiflora caerulea* L.	1	48.8	24.6	26.6	bees	wasps, hummingbirds	3	Morales 1999
Phytolaccaceae	*Phytolacca dioica* L.	0	0	30	70	moths	bees, flies	3	Bernardello et al. 1993
Plumbaginaceae	*Plumbago caerulea* Kuntze	0.3	23.9	22.8	53.3	flies	bees, butterflies	3	Galetto 1993
Rhamnaceae	*Condalia* x *montana* A. Cast.	2.6	68.9	17.6	13.5	flies	bees, butterflies, wasps, beetles	5	Morales 1999
Scrophulariaceae	*Agalinis genistifolia* (Cham. & Schltdl.) D'Arcy	0.3	21.8	38.9	39.2	bees		1	Galetto 1995c
	Mimulus luteus L.	0.1	5.6	46.2	48.1	bees		1	Galetto 1995c
Solanaceae	*Cestrum parqui* L'Herit.	0.5	28.9	37	34	moths	hummingbirds, butterflies	3	Galetto 1993
	Jaborosa integrifolia Lam.	0	0	48.7	51.3	moths		1	Vesprini and Galetto 2000
	Lycium americanum Jacq.	0	0	36.4	63.5	bees	butterflies, flies	3	Galetto et al. 1998
	L. cestroides Schltdl.	0.5	35.4	43.2	21.3	hummingbirds	butterflies, bees, flies	4	Galetto et al. 1998
	L. ciliatum Schltdl.	0.005	0.5	38.5	60.9	bees	flies	2	Galetto et al. 1998
	L. chilense Bertero	0.01	1.2	38.9	59.9	bees		1	Galetto et al. 1998
	L. elongatum Miers	0.001	0.1	28.5	71.3	bees		1	Galetto et al. 1998
	L. gilliesianum Miers	0.03	2.9	37	60.1	butterflies	bees	2	Galetto et al. 1998
	L. infaustum Miers	0.002	0.2	33.1	66.6	bees	flies, butterflies	3	Galetto et al. 1998

Appendix 1 (continued)

	L. nodosum Miers	0.002	1.5	47.9	50.5	bees		1	Galetto et al. 1998
	L. tenuispinosum Miers	0.02	1.7	36.6	61.6	flies	bees	2	Galetto et al. 1998
	L. vimineum Miers	0.02	2.1	30.1	67.7	moths	bees	2	Galetto et al. 1998
	Nicotiana glauca Graham	0.9	48.6	38.9	13.2	hummingbirds		1	Galetto 1991
	N. longiflora Cav.	0.7	41.5	24.3	34.1	moths		1	Galetto 1991
	N. noctiflora Hook.	0.2	16.9	43.5	39.5	moths		1	Galetto 1991
	Petunia axillaris (Lam.) Britton, Stern & Poggenb.	0.11	10	39	49.8	moths		1	Galetto 1993
	Salpichroa origanifolia (Lam.) Thell.	1.3	56.2	23.6	20.2	bees		1	Galetto et al. 1999
Verbenaceae	*Aloysia gratissima* (Gill. & Hook.)	0.8	27.3	39.5	31.8	bees	butterflies, flies	3	Galetto 1993
	Glandularia laciniata (L.) Schnack & Covas	0.4	16.7	44.4	38.8	butterflies		1	Galetto 1993
	G. peruviana (L.) Small	0.7	27	37.2	35.7	butterflies		1	Galetto 1993
	Lippia junelliana (Moldenke) Troncoso	0.4	20.2	31.1	48.2	butterflies	bees, flies	3	Galetto 1993
Zygophyllaceae	*Pourlieria microphylla* (Baill.) Desc., O'Donn. & Lourt.	0.15	12.6	46.7	40.7	flies	butterflies, bees, wasps	4	Morales 1999

Appendix 2. Analysed species from the Argentinean Patagonia region, indicating nectar sugar ratio (sucrose/fructose + glucose), percentages of sucrose, fructose, and glucose in nectar, floral visitors, and literature from where data were taken

Family	Taxon	Sugar ratio	% sucrose	% fructose	% glucose	Main floral visitors	Literature
Asteraceae	*Mutisia retrorsa* Cav.	0.01	1.16	40.23	57.7	bees	Bernardello et al. 1999
Fabaceae	*Adesmia ameghinoi* Speg.	0.02	2.33	42.36	55.31	bees	Bernardello et al. 1999
	A. candida Hook. f.	0.004	0.4	46.8	52.7	bees	Forcone et al. 1997, Bernardello et al. 1999
	A. corymbosa Clos	0.43	0	69.5	30.49	bees	Bernardello et al. 1999
	A. filipes A. Gray	0.002	0.2	38.2	61.6	bees	Forcone et al. 1997
	A. lotoides J. D. Hook.	0.04	4.1	41.36	54.54	bees	Bernardello et al. 1999
	A. muricata (Jacq.) DC.	0.003	0.3	43.2	56.5	bees	Forcone et al. 1997
	A. obcordata Clos	0	0	44.13	55.86	bees	Bernardello et al. 1999
	A. serrana Correa	0.018	1.8	42.9	55.3	bees	Forcone et al. 1997
	A. villosa J. D. Hook. f.	0.02	1.99	42.05	55.96	bees	Bernardello et al. 1999
	A. volkmanni Phil.	0.015	1.5	40.7	57.7	bees	Forcone et al. 1997, Bernardello et al. 1999
	Anarthrophyllum rigidum (Hook. & Arn.) Hieron.	0.026	2.6	39.1	58.3	bees	Forcone et al. 1997
	Astragalus cruckshanksii (Hook. & Arn.) Griseb.	0.02	2.24	43.63	54.12	bees	Forcone et al. 1997, Bernardello et al. 1999
	Glycyrrhiza astragalina Gill. ex Hook. & Arn.	0.99	49.47	28.02	22.52	bees	Bernardello et al. 1999
	Hoffmannseggia erecta Phil.	0.09	8.01	36.85	55.14	bees	Bernardello et al. 1999
	H. trifoliata Cav.	0.057	5.4	39.2	55.3	bees	Forcone et al. 1997
Frankeniaceae	*Frankenia patagonica* Speg.	0.003	0.3	47.5	52.2	flies	Forcone et al. 1997
Iridaceae	*Sisyrinchium junceum* Presl	0.405	28.8	26.3	44.8	bees	Forcone et al. 1997

Appendix 2 (continued)

Family	Taxon	Sugar ratio	% sucrose	% fructose	% glucose	Main floral visitors	Literature
Loasaceae	*Loasa argentina* Urb. & Gilg. in Speg.	0.283	22.3	32.9	45.8	bees	Forcone et al. 1997
Nyctaginaceae	*Bougainvillea spinosa* (Cav.) Heimerl	0.042	4.1	37.9	57.9	moths	Forcone et al. 1997
Oleaceae	*Menodora robusta* (Benth.) A. Gray	0.067	6.3	41	52.7	bees	Forcone et al. 1997
Onagraceae	*Oenothera bahia-blancae* W. Dietrich	27.6	96.46	1.81	1.73	moths	Bernardello et al. 1999
	Oe. magellanica Phil.	4.917	83.1	11.8	5.1	moths	Forcone et al. 1997
	Oe. mendocinensis Gill. ex Hook. & Arn.	20	94.51	3.2	2.28	moths	Bernardello et al. 1999
	Oe. odorata Jacq.	5.41	84.4	9.2	6.4	moths	Forcone et al. 1997
	Oe. rivadaviae W. Dietrich	19.408	95.1	3.8	1.1	moths	Forcone et al. 1997
	Oe. stricta Ledeb. ex Link	0.009	0.9	41.9	57.1	moths	Forcone et al. 1997
Polygalaceae	*Bredemeyera microphylla* (Griseb.) Hieron. ex Lorentz & Niederl.	0.01	0.58	44.22	55.2	bees	Bernardello et al. 1999
Rhamnaceae	*Discaria articulata* (Phil.) Miers	0	0	38.13	61.86	bees	Bernardello et al. 1999
	Retanilla patagonica (Speg.) Tortosa	0	0	60.4	39.6	bees	Forcone et al. 1997
Rubiaceae	*Oreopolus glacialis* (Poepp.) Ricardi	0.02	1.92	46.58	51.51	moths	Bernardello et al. 1999
Santalaceae	*Arjona tuberosa* Cav.	0.042	4.1	39.4	56.4	Butterflies	Forcone et al. 1997
Solanaceae	*Fabiana denudata* Miers	0	0	40.3	59.7	moths	Forcone et al. 1997
	F. patagonica Speg.	0.453	31.2	27.5	41.3	moths	Forcone et al. 1997
	Nicotiana petunioides (Griseb.) Millán	0.295	22.8	28.9	48.3	moths	Forcone et al. 1997
Tropaeolaceae	*Magallana porifolia* Cav.	0.029	2.9	31.7	65.3	bees	Forcone et al. 1997
Verbenaceae	*Glandularia aurantiaca* (Speg.) Botta	0.77	39.47	27.25	33.28	Butterflies	Bernardello et al. 1999
	G. crithmifolia (Gill. & Hook.) Covas & Schnack	0.002	0.2	44.2	55.6	Butterflies	Forcone et al. 1997
	G. flava (Gill. & Hook.) Covas & Schnack	0.412	29.2	34.4	36.4	Butterflies	Bernardello et al. 1999
	G. macrosperma (Speg.) Troncoso	0.05	4.51	42.96	52.53	Butterflies	Bernardello et al. 1999

Appendix 2 (continued)

Family	Taxon	Sugar ratio	% sucrose	% fructose	% glucose	Main floral visitors	Literature
	Junellia connatibracteata (O. Kuntze) Moldenke	0.01	0.59	43.43	55.98	Butterflies	Bernardello et al. 1999
	J. juniperina (Lagasca) Moldenke	0	0	42.8	57.2	Butterflies	Bernardello et al. 1999
	J. ligustrina (Lagasca) Moldenke	0.067	6.3	37.9	55.8	Butterflies	Forcone et al. 1997
	J. mulinoides (Speg.) Moldenke	0.011	1.1	41	57.8	Butterflies	Forcone et al. 1997, Bernardello et al. 1999
	J. thymifolia (Lagasca) Moldenke	0.02	2.09	43.13	54.77	Butterflies	Bernardello et al. 1999
	J. tridens (Lagasca) Moldenke	0	0.3	41.8	57.9	Butterflies	Bernardello et al. 1999
Zygophyllaceae	*Larrea divaricata* Cav.	0.01	1	41.9	57.1	bees	Forcone et al. 1997
	L. nitida Cav.	0.014	1.4	39.7	58.9	bees	Forcone et al. 1997

References

Armbruster W. S. (1996) Evolution of floral morphology and function: an integrative approach to adaptation, constraint, and compromise in *Dalechampia* (Euphorbiaceae). In: Lloyd D. G., Barrett S. C. H. (eds.) Floral biology: studies on floral evolution in animal-pollinated plants. Chapman & Hall, New York, pp. 241–272.

Ashworth L., Galetto L. (2001) Pollinators and reproductive success of a wild cucurbit adapted to disturbed habitats: *Cucurbita maxima* ssp. *andreana* (Cucurbitaceae). Plant Biol. 3: 398–404.

Baker H. G., Baker I. (1975) Studies of nectar-constitution and pollinator–plant coevolution. In: Gilbert L. E., Raven P. H. (eds.) Coevolution of animals and plants. Columbia University Press, New York, pp. 126–152.

Baker H. G., Baker I. (1983a) Floral nectar sugar constituents in relation to pollinator type. In: Jones C. E., Little R. J. (eds.) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp. 117–141.

Baker H. G., Baker I. (1983b) A brief historical review of the chemistry of floral nectar. In: Bentley B., Elias T. S. (eds.) The biology of nectaries. Columbia University Press, New York, pp. 127–152.

Baker H. G., Baker I. (1990) The predictive value of nectar chemistry to the recognition of pollinator types. Israel J. Bot. 39: 157–166.

Baker H. G., Baker I., Hodges S. A. (1998) Sugar composition of nectars and fruits consumed for birds and bats in the tropics deciduous forests. Biotropica 30: 559–586.

Bernardello G., Galetto L., Anderson G. J. (2000) Floral nectary structure and nectar chemical composition of some species from Robinson Crusoe Island (Chile). Canad. J. Bot. 78: 862–872.

Bernardello G., Galetto L., Forcone A. (1999) Floral nectar chemical composition of some species from Patagonia II. Biochem. Syst. Ecol. 27: 779–790.

Bernardello L., Galetto L., Juliani H. R. (1991) Nectar and nectary structure in some Argentinean *Bromeliaceae*. Ann. Bot. 67: 401–411.

Bernardello L., Galetto L., Juliani H. R. (1993) Néctar, nectario y visitantes florales en *Phytolacca dioica* (Phytolaccaceae). Revista Brasil. Bot. 16: 9–15.

Bleiweiss R. (1998) Origin of hummingbird faunas. Biol. J. Linn. Soc. 65: 77–97.

Cabrera A. L. (1971) Fitogeografía de la República Argentina. Bol. Soc. Argent. Bot. 14: 1–42.

Cocucci A. A., Galetto L., Sérsic A. (1992) El síndrome floral de *Caesalpinia gilliesii* (Fabaceae – Caesalpinioideae). Darwiniana 31: 111–135.

Dafni H., Lensky Y., Fahn A. (1988) Flower and nectar characteristics of nine species of Labiatae and their influence on honeybee visits. J. Apic. Res. 27: 103–114.

Downs C. T., Perrin M. R. (1996) Sugar preferences of some southern African nectarivorous birds. Ibis 138: 455–459.

Elisens W. J., Freeman C. E. (1988) Floral nectar sugar composition and pollinator type among New World genera in tribe Antirrhineae (Scrophulariaceae). Amer. J. Bot. 75: 971–978.

Forcone A., Galetto L., Bernardello L. (1997) Floral nectar chemical composition of some species from Patagonia. Biochem. Syst. Ecol. 25: 395–402.

Freeman C. E., Reid W. H., Becvar J. E., Scogin R. (1984) Similarity and apparent convergence in the nectar-sugar composition of some hummingbird-pollinated flowers. Bot. Gaz. 145: 132–135.

Freeman C. E., Worthington R. D. (1985) Some floral nectar-sugar compositions of species from southeastern Arizona and southwestern New Mexico. Madroño 32: 78–86.

Freeman C. E., Worthington R. D., Corral R. D. (1985) Some floral nectar-sugar compositions from Durango and Sinaloa, Mexico. Biotropica 17: 309–313.

Freitas L., Bernardello G., Galetto L., Paoli A. A. S. (2001) Nectaries and reproductive biology of *Croton sarcopetalus* (Euphorbiaceae). Bot. J. Linn. Soc. 136: 267–277.

Galen C. (1996) The evolution of floral form: insights from an Alpine wildflower, *Polemonium viscosum* (Polemoniaceae). In: Lloyd D. G., Barrett S. C. H. (eds.) Floral biology: studies on floral evolution in animal-pollinated plants. Chapman and Hall, New York, pp. 273–291.

Galetto L. (1991) Sobre el néctar y los nectarios de algunas especies de *Nicotiana* (Solanaceae). Kurtziana 21: 165–176.

Galetto L. (1993) Estudios sobre el néctar en Asteridae argentinas: análisis químico e histología comparada de las estructuras secretoras. Tesis Doctoral, Universidad Nacional de Córdoba, Argentina.

Galetto L. (1995a) Estudios sobre el néctar y los nectarios en *Hyaloseris rubicunda* y *Barnadesia odorata* (Asteraceae-Mutisieae). Darwiniana 33: 127–133.

Galetto L. (1995b) Nectary structure and nectar characteristics in some Bignoniaceae. Plant Syst. Evol. 196: 99–121.

Galetto L. (1995c) Estructura del nectario y composición química del néctar en cuatro especies de Scrophulariaceae. Kurtziana 24: 105–118.

Galetto L. (1997) Flower structure, nectar chemical composition in three Argentine Apocynaceae. Flora 192: 197–207.

Galetto L., Bernardello G., Rivera G. (1997) Nectar, nectaries, flower visitors, and breeding system in five terrestrial Orchidaceae from central Argentina. J. Plant Res. 110: 393–403.

Galetto L., Bernardello G., Isele I., Vesprini J. L., Speroni G., Berduc A. (2000) Reproductive biology of *Erythrina crista-galli* (Fabaceae). Ann. Missouri Bot. Gard. 87: 127–145.

Galetto L., Bernardello G., Sosa C. A. (1998) The relationship between floral nectar composition and visitors in *Lycium* (Solanaceae) from Argentina and Chile: what does it reflect? Flora 193: 303–314.

Galetto L., Bernardello L. M., Juliani H. R. (1990) Acerca del nectario, néctar y visitantes florales en *Ligaria cuneifolia* (Loranthaceae). Darwiniana 30: 155–161.

Galetto L., Bernardello L. M., Juliani H. R. (1993) Estructura del nectario, composición química del néctar y mecanismo de polinización en tres especies de *Siphocampylus* (Campanulaceae). Kurtziana 22: 81–96.

Galetto L., Morales C. L., Torres C. (1999) Biología reproductiva de *Salpichroa origanifolia* (Solanaceae). Kurtziana 27: 211–224.

Gottsberger G., Schrauwen J., Linskens H. F. (1984) Amino acids and sugars in nectar, and their putative evolutionary significance. Plant Syst. Evol. 145: 55–77.

Jausoro M., Galetto L. (2000) Estudio comparativo de nectario y néctar en flores perfectas y estaminadas de *Caesalpinia gilliesii* (Fabaceae-Caesalpinoideae). Bol. Soc. Argent. Bot. 35: 107–114.

Kevan P.G., Baker H.G. (1999) Insects on flowers. In: Huffaker C. B., Elias A. P. (eds.) Ecological entomology, 2nd edn. John Wiley & Sons, New York, pp. 553–584.

López H., Galetto L. (2002) Flower structure and reproductive biology of *Bougainvillea stipitata* (Nyctaginaceae). Plant Biol. 4: 508–514.

Martínez del Río C. (1990) Sugar preferences in hummingbirds: the influence of subtle chemical differences on food choice. Condor 92: 1022–1030.

Martínez del Río C., Stevens B. R., Daneke D. E., Andreadis P. T. (1988) Physiological correlates of preference and aversion for sugars in three species of birds. Physiol. Zool. 61: 222–229.

Morales M. (1999) Selección de caracteres florales por polinizadores, en especies del Bosque Serrano (Chaco Serrano). Undergraduate Thesis. Universidad Nacional de Córdoba.

Percival M. S. (1961) Types of nectar in angiosperms. New Phytol. 60: 235–281.

Perret M., Chautems A., Spichiger R., Peixoto M., Savalainen V. (2001) Nectar sugar composition in relation to pollination syndromes in Sinningieae (Gesneriaceae). Ann. Bot. 87: 267–273.

Pham-Delegue M. H., Etievant P., Guichard E., Marilleau R., Douault Ph., Chauffaille J., Masson C. (1990) Chemicals involved in honeybee–sunflower relationship. J. Chem. Ecol. 16: 3053–3065.

Proctor M., Yeo P., Lack A. (1996) The natural history of pollination. Timber Press, Portland, Oregon.

Silvertown J., Dodd M. (1997) Comparing plants and connecting traits. In: Silvertown J., Franco M., Harper J. L. (eds.) Plant life histories. The Royal Society University Press, Cambridge, pp. 3–16.

Sokal R. R., Rohlf F. J. (1995). Biometry. W. H. Freeman, San Francisco, California.

Southwick E. E., Loper G. M., Sadwick S. E. (1981) Nectar production, composition, energetics and pollinator attractiveness in spring flowers of western New York. Amer. J. Bot. 68: 994–1002.

SPSS Inc. (1992) SPSS for Windows: base system user's guide, Release 5.0. SPSS Inc., Chicago.

Stiles F. G., Freeman C. E. (1993) Patterns in floral nectar characteristics of some bird-visited plant species from Costa Rica. Biotropica 25: 191–205.

Stromberg M.R., Johnsen P.B. (1990). Hummingbird sweetness preferences: taste or viscosity? Condor 92: 606–612.

Sweeley E. C., Bentley R., Makita M., Wells W.W. (1963) Gas liquid chromatography of trimethylsilyl derivatives of sugars and related substances. J. Amer. Chem. Soc. 85: 2497–2507.

Torres C., Galetto L. (2002) Are nectar-sugar composition and corolla-tube length related to the diversity of insects that visit Asteraceae flowers? Plant Biol. 4: 360–366.

Vesprini J. L., Galetto L. (2000) The reproductive biology of *Jaborosa integrifolia* (Solanaceae): why its fruits are so rare? Plant Syst. Evol. 225: 15–28.

van Wyk B. E. (1993) Nectar sugar composition in Southern African Papilionoideae (Fabaceae). Biochem. Syst. Ecol. 21: 271–277.

van Wyk B. E., Whitehead C. S., Glen H. F., Hardy D. S., van Jaarsveld E. J., Smith G. F. (1993) Nectar sugar composition in the subfamily Alooideae (Asphodelaceae). Biochem. Syst. Ecol. 21: 249–253.

Address of the authors: Leonardo Galetto (e-mail: leo@imbiv.unc.edu.ar) and Gabriel Bernardello (e-mail: bernarde@imbiv.unc.edu.ar), Instituto Multidisciplinario de Biología Vegetal, Casilla de Correo 495, 5000 Córdoba, Argentina.