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Potential use of floral nectar sugar characteristics in plant selection for pollinator habitats

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ABSTRACT

The use of urban green spaces, including gardens, in pollinator conservation initiatives, excites significant public interest but advice on effective plants frequently relies on qualitative data. This study considered pollinator responses to specific nectar sugar characteristics to determine if they offer the potential for the selection of candidate plants. Pollinator feeding on 60 plant species at the National Botanic Garden of Wales was related to their nectar characteristics to investigate response consistency at different taxonomic levels. The feeding frequency of Hymenoptera, particularly the social Hymenoptera, was significantly correlated with the volume of nectar offered by flowers, but greater differentiation between plant species occurred when specific nectar sugar characteristics were considered. Feeding was significantly correlated with the volume of the hexose monosaccharides glucose or fructose for the Hymenoptera, particularly the social Hymenoptera (and for the two social genera analysed individually, *Apis* spp. *Bombus* spp.), but not for non-social species. Similarly, feeding visits were correlated with the percentage of glucose or fructose in nectar in the Hymenoptera, social Hymenoptera and non-social groups (including three individual genera tested (*Apis spp.*, primitively eusocial *Lasioglossum*, and non-social *Andrena* spp.). Fewer and less consistent outcomes were recorded when the (disaccharide) sucrose content of nectar was investigated. In comparative analyses conducted for other pollinator groups (Diptera and Lepidoptera), feeding was only found to be correlated with glucose content. The social Hymenoptera are a particular focus of gardeners and the use of percentage glucose or fructose in nectar is discussed as a potential component of a screening approach to identify keystone plant species.

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Introduction

The decline in wild and managed pollinator abundance and diversity, particularly in industrialized countries, is well documented in North America and North-West Europe and although more limited data is available elsewhere, is thought to be a feature of many natural and farmed environments globally (Ollerton et al., 2014; Steffan-Dewenter et al., 2005; Vanbergen & The Insect Pollinators Initiative, 2013). The primary contributing factors to pollinator decline include habitat loss and landscape change, often resulting from changing agricultural practices (Steffan-Dewenter et al., 2005).

Nectar produced by flowers is a keystone resource exploited by a wide range of pollinators in terrestrial ecosystems. Groups such as bumble bees, honey bees and solitary bees also utilize pollen, which is exploited for a range of nutritional components (Moerman et al., 2017; Ryder et al., 2021; Wäckers et al., 2007). Nectar is an aqueous solution, containing the disaccharide sucrose, and the hexose monosaccharides glucose and fructose, together with smaller amounts of other sugars and organic and inorganic compounds (Baker & Baker, 1983). Characteristics such as sucrose–hexose proportions, sugar concentration and composition, and volume and time of nectar secretion vary between and within plant species, are known to affect pollinator behavior and species diversity, and consequently pollination efficiency and plant reproduction (Baude et al., 2016; Herrera, 2009; Herrera et al., 2006; Lanza et al., 1995; Pacini et al., 2003; Perret et al., 2001; Petanidou, 2005; Rathcke, 1992; Wäckers et al., 2007; Waddington, 2001; Wolff et al., 2006). Convergences between taxonomically unrelated plant species in their nectar characteristics are considered to be adaptations to pollinator sugar intake, digestion efficiencies or preferences of specific (taxonomically diverse) pollinators (Haber & Frankie, 1989). Variation in nectar traits is also affected by extrinsic abiotic and biotic factors unrelated to the plants and can

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Table 1. Floral nectar characteristics of the plant species investigated.

Species	Nectar Vol	Gluc Vol	% Gluc	Fruc Vol	% Fruc	Suc Vol	% Suc	Species	Nectar Vol	Gluc Vol	% Gluc	Fruc Vol	% Fruc	Suc Vol	% Suc
H. helix	1.48 (0.15)	0.39	26	0.18	12	0.03	2	*F. japonica*	0.38 (0.11)	0.12	32	0.13	34	0.08	22
I. aquifolium	0.56 (0.08)	0.22	41	0.26	46	0.07	12	*T. pratense*	0.24 (0.06)	0.02	10	0.03	14	0.16	68
H. nonscripta	0.09 (0.01)	0.03	31	0.07	25	0.01	9	*L. odoratus*	1.82 (0.24)	0.09	5	0.2	11	0.66	36
D. maculata	0 (0)	0	0	0	0	0	0	*G. pratense*	0.53 (0.11)	0.09	17	0.10	18	0.14	26
C. glomerata	0.88 (0.18)	0.02	2	0.01	10	0.04	4	*B. davidii*	1.32 (0.10)	0.11	8	0.12	9	0.32	24
C. nigra	1.88 (0.03)	0.43	24	0.47	25	0.9	48	*A. reptans*	0.74 (0.09)	0.03	4	0.19	25	0.09	12
S. jacobaea	0.08 (0.03)	<.01	3	<.01	3	<.01	1	*D. purpurea*	6.88 (0.21)	0.14	2	0.41	6	1.10	16
B. perennis	0 (0)	0	0	0	0	0	0	*V. chamaedrys*	0.06 (0.01)	0.01	11	0.01	9	<.01	1
T. officinale agg.	2.46 (0.42)	1.06	43	0.98	40	0.15	6	*V. officinalis*	0.59 (0.14)	0.07	12	0.14	24	0.07	11
C. rotundifolia	0.28 (0.05)	0.03	12	0.07	26	0.03	11	*S. sylvatica*	1.45 (0.27)	0.25	17	0.46	32	0.32	22
C. palustre	0.23 (0.01)	0.04	15	0.07	30	0.12	53	*P. sylvatica*	0.62 (0.11)	0.03	5	0.17	28	0.4	64
L. vulgare	0 (0)	0	0	0	0	0	0	*O. vulgare*	0.69 (0.08)	0.07	10	0.08	12	0.16	23
H. annuus	6.50 (0.49)	2.08	32	2.21	34	0.2	3	*S. pratensis*	0.66 (0.17)	0.05	8	0.11	13	0.25	38
A. officinalis	0.66 (0.12)	0.27	41	0.28	43	0.03	4	*O. vernus*	0.3 (0.03)	0.03	10	0.06	20	0.04	14
B. officinalis	2.91 (0.54)	0.35	12	0.26	9	1.34	46	*M. aquatica*	6.08 (0.19)	-	-	-	-	-	–
S. officinale	2.19 (0.5)	0.02	1	0.13	6	0.59	27	*L. galeobdolon*	0.51 (0.12)	0.04	7	0.1	20	0.25	48
E. vulgare	2.25 (0.24)	0.18	8	0.18	8	1.4	62	*V. reichenbachiana*	0.80 (0.10)	0.37	46	0.43	54	0	0
B. napus	0.13 (0.02)	0.07	53	0.06	44	<.01	2	*V. arvensis*	0.08 (0.01)	<.01	2	<.01	4	<.01	3
C. flexuosa	0.12 (0.05)	0.02	14	0.02	15	<.01	2	*E. hirsutum*	0.84 (0.11)	0.25	30	0.27	32	0.02	2
L. flos-cuculi	0.77 (0.11)	0.04	5	0.09	11	0.09	11	*L. salicaria*	0.49 (0.09)	0.06	12	0.06	12	0.08	16
S. dioica	0.79 (0.22)	0.06	7	0.10	13	0.12	15	*C. angustifolium*	1.09 (0.12)	0.16	15	0.22	20	0.43	39
K. arvensis	1.25 (0.19)	0.45	36	0.43	34	0.28	22	*O. acetosella*	0.08 0.01)	0.02	30	0.03	31	0	0
L. periclymenum	5.53 (0.68)	0.39	7	0.55	10	3.76	68	*P. spinosa*	0.25 (0.05)	0.11	44	0.11	43	0.01	4
E. cinerea	1.77 (0.14)	0.09	5	0.21	12	0.25	14	*R. fruticosus*	3.67 (0.23)	0.88	24	0.88	24	1.03	28
E. nigrum	0.57 (0.08)	0.26	45	0.26	45	0	0	*C. monogyna*	0.29 (0.05)	0.05	17	0.46	16	0.03	9
I. glandulifera	0.48 (0.07)	0.01	1	0.01	3	0.05	11	*A. hippocastanum*	0.53 (0.06)	0.02	4	0.02	4	0.2	38
P. vulgaris	1.85 (0.42)	0.54	29	0.52	28	0.57	31	*A. pseudoplatanus*	1.44 (0.27)	0.07	5	0.12	8	0.17	12
R. ponticum	1.14 (0.15)	0	0	0	0	0.88	77	*C. arvensis*	0.62 (0.14)	0.05	8	0.09	14	0.24	39
L. corniculatus	0.47 (0.07)	0.13	28	0.15	31	0.19	41	*S. nigrum*	2.59 (0.36)	0.21	8	0.36	14	1.01	39
V. faba	7.20 (1.13)	0.58	8	1.01	14	2.8	39	*S. tuberosum*	0.11 (0.02)	<.01	1	<.01	1	0	0

Mean (± SE) total nectar volume (μL) per flower, and volume (μL) or percentage of glucose (Gluc), fructose (Fruc) or sucrose (Suc). Data corrected to 2 decimal places; – = no data due to broken Fallon tube).

result in regional differences in plant–pollinator interactions, potentially requiring datasets to be collected from different regions to support the optimal selection of conservation resources (Herrera, 2009).

The potential for creating a network of habitats using urban green spaces to contribute to the mitigation of pollinator declines has been promoted by a range of conservation organizations (Goddard et al., 2010; Levé et al., 2019; Rollings & Goulson, 2019). In common with wild plants, the attraction of pollinators to ornamental plant species and varieties is variable and although advice on effective species to use in the creation of pollinator habitats is available from many sources, it is frequently based on qualitative assessments of pollinator behavior, leading to inconsistencies (Garbuzov & Ratnieks, 2014).

Further quantitative investigations supporting the selection of plants for use in urban pollinator habitats have been called for (Rollings & Goulson, 2019) but the large number of candidate plant species precludes reliance on resource intensive behavioral screening experiments. An alternative approach that offers a more rapid screening procedure might be based on the specific plant characteristics that affect pollinator behavior and colony/population success but relies on an improved understanding of specific characteristics of nectar and pollen rewards offered by flowers that preferentially attract pollinators (Ryder et al., 2021).

This study investigated the nectar sugar characteristics of 60 plant species grown at the National Botanic Garden in South Wales and related the data to pollinator feeding visits recorded in the field. The hypothesis that pollinator feeding responses to nectar sugar characteristics are sufficiently consistent to justify their inclusion as a component of a screening process supporting plant species selection for conservation initiatives was tested.

Materials and methods

Field site

Field work was undertaken at the National Botanic Gardens of Wales (SN520180) in 2018 (June-September) and 2019 (April-May). The gardens are established on a 230 ha site comprised of formal and semi-formal flower beds, wild flower meadows, mixed woodland, and the 130 ha Waun Las national nature reserve, and are surrounded by grassland for mixed livestock farms. Nectar sampling and pollinator assessments were undertaken in the formal area of the gardens.

Floral selection

The flowering plant species studied were selected from a list collectively estimated to provide 98% of the floral resource in the UK (Baude et al., 2016; Fitter & Peat, 1994). Flower species that do not offer a nectar resource were deleted and those remaining were divided according to the month(s) in which they flower. A total of ten species (spanning a range

Table 2. Correlations between the number of pollinator feeding visits to flowers of 60 plant species and either the volume, or percentage of glucose, fructose or sucrose offered in the nectar.

Group	Sugar metric	Glucose		Fructose		Sucrose	
		r_s	$p <$	r_s	$p <$	r_s	$p <$
Hymenoptera	Volume	0.40	0.01	0.35	0.01	–	–
Social Hymenoptera	Volume	0.40	0.01	0.38	0.01	0.31	0.05
Apis	Volume	0.38	0.01	0.28	0.05	–	–
Bombus	Volume	0.26	0.05	0.32	0.05	0.32	0.05
Hymenoptera	Percentage	0.36	0.01	0.30	0.05	–	–
Social Hymenoptera	Percentage	0.28	0.05	0.26	0.05	0.26	0.05
Non-Social Hymenoptera	Percentage	0.42	0.001	0.25	0.05	0.3	0.05
Apis	Percentage	0.37	0.01	–	–	–	–
Bombus	Percentage	–	–	–	–	0.28	0.05
Lasioglossum	Percentage	0.29	0.05	–	–	–	–
Andrena	Percentage	0.32	0.05	–	–	0.26	0.05
Diptera	Volume	0.30	0.05	–	–	–	–
	Percentage	0.37	0.01	–	–	–	–
Lepidoptera	Volume	0.33	0.01	–	–	–	–
	Percentage	0.28	0.05	–	–	–	–

r_s = Spearman rank correlation coefficient and associated significance (p); degrees of freedom = 57 in each case to take account of a lost sample resulting from a broken Fallon tube (see Table 1); – = no statistically significant relationship ($p > 0.05$) identified.

of orders and families) which flowered in each month of the study period were randomly selected for the assessment using the RAND function of Microsoft Excel (Windows, USA), and no species was investigated in more than a single month (see Supplementary material, Table S1).

Pollinator foraging

Pollinator foraging assessments were undertaken on days when daytime temperatures exceeded the average 30-year mean temperature for the month in which the assessment was conducted, and no rain was forecast. Assessments were taken between 10:00 and 17:00, with the sampling period divided into hourly slots to facilitate a timed survey approach (Dafni, 1992). Each plant species was observed for a total of 50 min (five 10-min assessments) with each assessment made during a different hourly slot to account for potential diurnal variation in foraging. As the sampling schedule limited the number of plant species that could be assessed during a single day, observations were made over two adjacent days. The days and the hourly assessment slots for each plant species were selected at random.

Foraging visits to 20 individual floral units growing in close proximity to, but excluding plants from which nectar samples had previously been taken (see below), were assessed within a maximum of two days of the nectar assessment. The number of feeding visits by each pollinator species (defined as the insect settling on the flower and extending its mouthparts into the nectary) observed within each 10-min time slot was recorded. The pollinator species were either identified to genus visually, or the insect was photographed or captured with a net for later identification. (Ball & Morris, 2015; Falk, 2015; Lewington, 2017).

Nectar sampling

To avoid nectar depletion resulting from insect feeding, between 18:00 and 20:00 on the evening preceding the sampling of each plant species, 20 undamaged flowers (open and showing no sign of senescence) were netted using a cotton fabric (1.4×1.7 mm weave; Baude et al., 2016).

Nectar sampling was conducted during randomly assigned time slots between 08:00 and 10:00 the following day using 1 or 5 μL micro capillaries (Hirschmann® minicaps®, Hauptstraße). The micro capillaries were placed in Falon tubes and returned to the laboratory on ice in a cold box. The volume of nectar taken from each floral unit (defined as one flower; Fornoff et al., 2017) was recorded, before samples from each plant species were combined to provide sufficient nectar for chemical analysis (Chalcoff et al., 2006). The combined sample was stored in a laboratory freezer (−20 °C; Arctiko ltfe 290®, Oddesundvej), to control for the effects of storage time on sugar ratios (Morrant et al., 2009).

The plants sampled included compound flowers, on which individual pollinators typically fed from multiple florets at each visit. As this will affect the volume of nectar available to pollinators, in these cases preliminary sampling at the experimental site was undertaken (using the above technique), to determine the average number of florets probed during an individual pollinator visit to a floral unit. The species and size of the pollinators affected the number of florets probed, with larger insects (>8 mm) consistently feeding on a mean of 25.1 ± 1.2 florets at each visit, and smaller species from a mean of 5 ± 0.7 florets. The most commonly encountered pollinator genera (those used in subsequent statistical analysis of responses at the genus level) were classed as large and represented 75.59% of the total number of individuals observed during the study (Supplementary material, Table S2), and the nectar from 25 florets was sufficient for the chemical analysis. Thus, all assessments of nectar volume offered by a compound flower were defined as volume/25 florets.

Nectar sample preparation

Nectar samples taken from the freezer were maintained at room temperature for 30 min. Distilled water (400 μL) was added to the Falon tube and agitated (Ika vortex genius 3, Loughborough) to dissolve any nectar residue before the contents were transferred to a pestle and mortar, the micro capillary ground to a fine powder and the nectar solution pipetted into a microfuge tube. The glass powder was rinsed with a further 400 µL of distilled water, added to the microfuge tube and centrifuged (Heraeus Pico 21 centrifuge, Runcorn) at 80 rpm for 1 min to remove any residue. The supernatant was transferred to a pre-weighed microfuge tube and freeze dried (Labconco FreeZone, Kansas City).

HPAEC analysis

Separation and quantification of sugars were carried out using high performance anion exchange chromatography (HPAEC) in the laboratory of BEACON Wales (University of Aberystwyth, Wales) following the method of Lohaus and Schwerdtfeger (2014). Data were presented as the percentage of each sugar (glucose, sucrose and fructose) per unit volume of nectar.

Statistical analysis

Statistical analysis was conducted using R Version 4.0.2 (R Core Team, 2017).

The volume of fructose, glucose or sucrose per unit volume of nectar sample was calculated by multiplying the sugar percentage by the mean volume of nectar for each flower species. As diagnostic model plots and the Shapiro-Wilks tests showed the data were not normally distributed, Spearman rank correlation coefficient was used to investigate the relationship between the total number of visits by foraging pollinators to the different plant species and either the mean nectar volume offered by their flowers, or the volume or percentage of the hexose monosaccharide or disaccharide sugars present.

This analysis was also repeated for individual taxonomic groups or guilds including Hymenoptera, Diptera or Lepidoptera, social Hymenoptera, non-social Hymenoptera, and each of the seven individual genera for which sufficient data had been recorded (*Apis* spp., *Bombus* spp., *Lasioglossum* spp., *Andrena* spp., *Eristalis* spp., *Syritta* spp., *Melanostoma* spp.)

Results

A total of 2700 pollinators were recorded, principally from three orders, Hymenoptera (1732), Diptera (796) and Lepidoptera (134). In addition, sufficient numbers of four genera of Hymenoptera (*Apis*, *Bombus*, *Andrena*, *Lasioglossum*) and three of Diptera (*Eristalis*, *Syritta*, *Melanostoma)* were recorded to support individual statistical analysis (see Supplementary material, Table S2).

Response to nectar volume – Hymenoptera

Mean nectar volume per flower varied (0–7.2 µL per flower) between plant species (Table 1). There was a significant correlation between the total number of Hymenopteran feeding visits and the mean volume of nectar offered by flowers of different plant species ($r = 0.28$; d.f. = 58, $p < 0.05$). Within the Hymenoptera, the number of feeding visits made by social species was correlated with the mean nectar volume ($r = 0.32$, d.f. = 58, $p < 0.01$), but not in non-social species. A similar correlation was recorded for only one individual genus, *Bombus spp.* ($r = 0.27$, d.f. = 58, $p < 0.05$).

Response to hexose monosaccharide sugars in nectar – Hymenoptera

The mean volume of glucose offered by flowers varied between plant species (0–2.08 µL/flower), but exceeded 0.5 µL in only 5 of the 59 species assessed; correlations with pollinator feeding frequency were therefore reliant on a few data points at the higher end of the range making species selection for pollinator habitats more difficult (Table 1; Supplementary material, Figure S1). The percentage glucose content of nectar also varied widely between plant species (0–53%), but data points were distributed across the full range supporting a more accurate interpretation of relationships established with pollinator feeding frequency (Supplementary material, Figure S1).

Significant positive correlations occurred between the total number of Hymenopteran foraging visits to flowers and the volume of glucose present in nectar samples (Supplementary material, Figure S1; Table 2). Within the Hymenoptera a significant association between flower visits and glucose volume was also found in the social Hymenoptera, but not for non-social species, and reflecting this finding foraging intensity and glucose volume was correlated in only the individual social genera investigated (*Apis spp.* and *Bombus spp.*).

Significant positive correlations were recorded between glucose percentage, and total foraging visits by the Hymenoptera group, and both the social, and non-social groups separately (Supplementary material, Figure S1; Table 2). Frequency of flower feeding by the eusocial *Apis spp.*, primitively eusocial *Lasioglossum spp.* (Danforth, 2002), and non-social *Andrena spp.* were also positively related to the percentage glucose content of the nectar.

The volume of fructose offered by flowers varied between plant species (0–2.21 µL/flower) but only 6 of the 59 studied offered > 0.5 µL. The percentage fructose content of nectar also varied between plant species (Table 1), and in this case, data points were distributed evenly across the full range strengthening its use for species selection (Supplementary material, Figure S2).

The total number of flower visits made by all (total) Hymenopteran species recorded was significantly correlated with both the volume and percentage of fructose present in nectar samples Similarly, when data for the social bee and non-social bee groups were analysed separately, positive correlations with percentage fructose in nectar were recorded (Supplementary material, Figure S2; Table 2). However, in the non-social Hymenoptera, a similar relationship was not recorded with fructose volume. When individual genera were investigated, positive responses to fructose volume were found for *Apis spp.* and *Bombus spp.*, but no correlations with percentage fructose were found.

Response to the disaccharide sucrose – Hymenoptera

The mean nectar sucrose volumes offered by the flowers of the plant species studied also varied widely from 0 to 3.76 µL, but relatively few (11 of the 59) of the species assessed exceeded 0.5 µL per flower (Table 1). A slightly wider range of percentage sucrose content across species was recorded (0–77%), and data points were distributed evenly across the full range.

Less consistent responses to nectar sucrose were recorded. No significant relationship between feeding visit frequency and the percentage or volume of sucrose present in nectar samples was found when pooled data from the Hymenopteran group of species were analyzed (Table 2). When data for social Hymenoptera alone were investigated, however, significant associations between the visitation rate and sucrose content (both volume and percentage) were identified, reflecting in each case a similar response when data for *Bombus spp.* alone were analyzed. A foraging response to the percentage sucrose content of nectar was also recorded when data for non-social Hymenoptera and *Andrena* spp. were considered.

Responses of Diptera and Lepidoptera to nectar sugar characteristics

Potential foraging preferences were less evident in the Diptera and Lepidoptera. There were significant positive associations between the total number of Dipteran or Lepidopteran foragers making feeding visits to flowers, and both the percentage and volume of glucose present in the nectar of sampled flowers (Table 2). No similar significant relationships were found, however, when data for individual genera were analysed, or for the nectar fructose or sucrose characteristics. Similarly, no correlation between feeding frequency and total nectar volume offered by flowers was identified.

Discussion

A range of conservation initiatives is being developed to mitigate declining pollinator abundance and associated consequences for biodiversity and ecosystem services (Kleijn et al., 2018; Levé et al., 2019) and there is growing interest in utilizing urban green spaces, which collectively offer a matrix of interconnected florally rich pollinator habitats (e.g., Goddard et al., 2010; Levé et al., 2019). The success of the approach depends on the optimization of a number of factors including the range of plants grown, but most current advice supporting the selection of pollinator attractive species relies on qualitative data. There is therefore a need for widespread quantitative screening (Rollings & Goulson, 2019) but such studies of pollinator foraging behavior can be time consuming and resource intensive. Improved understanding of the nutritional characteristics of nectar and pollen that attract foraging insects may enable quicker identification of primary candidate plant species/varieties prior to detailed behavioral screening (Ryder et al., 2021).

Pollen and nectar are keystone resources exploited by pollinators in terrestrial ecosystems, with some species (such as bumble bees, honey bees and solitary bees) utilizing both (Wäckers et al., 2007). Pollen offers a range of nutritional components including proteins and their constituent amino acids, lipids, carbohydrates, and vitamins, with both their ratio and level being related to its nutritional value and thus the individual or colony success (Moerman et al., 2017; Ryder et al., 2021; Stabler et al., 2015).

Pollen characteristics alone may be insufficient, however, to predict flower utilization by pollinators, as nectar is also an important resource for many species. The disaccharide sucrose and the hexose monosaccharides glucose and fructose are the main nutritional constituents of nectar, with smaller amounts of other sugars and organic and inorganic compounds occurring (Baker & Baker, 1983). Wide inter- and intra-species variation in the main sugars offered by plants to pollinators has been recorded, and among other characteristics, sugar volume and concentration have been related to flower preferences of pollinators (Baker & Baker, 1983; Pacini et al., 2003; Wolff et al., 2006). The current study was a preliminary investigation comparing 60 plant species to test the hypothesis that pollinator feeding responses to nectar sugar characteristics are sufficiently consistent to justify their inclusion as a component of a screening process supporting plant species selection for conservation initiatives.

A significant positive relationship between feeding visits and the volume of nectar offered by flowers was established when data for all species of Hymenoptera recorded in the field study were combined. Similar relationships were found when the data from species of social Hymenoptera were considered in isolation, but not for the non-social Hymenoptera, or the dipteran or lepidopteran species investigated. However, greater differentiation was found when the sugar characteristics of nectar were investigated. A significant correlation was established between the number of flower feeding visits by all Hymenoptera species combined and the mean volume of each of the two hexose monosaccharide sugars (glucose and fructose) found in nectar. Once again, a similar response was only detected within social Hymenoptera. Although the volume of glucose and fructose offered in nectar influenced the floral preferences of social bees, the result should be treated with caution as the relationships were reliant on a few data points from flowers with higher nectar glucose or fructose volumes.

This constraint did not occur when the number of feeding visits was related to the percentage of glucose or fructose in nectar. In both cases, there was a significant correlation between the number of feeding visits by Hymenoptera and nectar sugar content, and within this group, for both social and non-social Hymenoptera. The result of an analysis of data for individual genera was consistent with the outcomes for glucose responses. Thus, overall, the percentage and volume of glucose in nectar displayed sufficient consistency in the correlation with flower feeding visits by social Hymenoptera to warrant further investigation as components of a screening process supporting plant species selection for pollinator conservation initiatives. Significant correlations were also identified between feeding visits and one metric (percentage glucose or fructose content of nectar) for the non-social Hymenoptera, which may also be utilized in screening.

Only weak ($p < 0.05$) and less consistent associations were recorded between feeding visits and the percentage of the disaccharide sucrose in nectar. Significant positive relationships were found for both social and non-social Hymenoptera (but not when data for all Hymenoptera were combined). Similar weak correlations with sucrose volume in floral nectar loads were recorded in the social Hymenoptera.

The results of this study support and extend those of previous work that has shown that plant pollinator behavior can be related to both the volume of nectar offered by flowers and its sugar composition. Such nectar sugar characteristics offered by plants growing in a local area have been related to pollinator species diversity and thus pollination efficiency (Wäckers et al., 2007). The consistent responses of social Hymenoptera, an important group of insect pollinators that are a focus of public attention, to percentages of the hexose monosaccharides in nectar may provide a useful component of a more efficient approach to screening plants for use in urban habitats (Herrera, 2009; Herrera et al., 2006; Lanza et al., 1995; Petanidou, 2005; Rathcke, 1992). The limitations of behavioral screening of a large number of plant species for use in pollinator conservation initiatives may be obviated by the initial selection of promising candidates using chemical analysis to establish the nutritional characteristics of the nectar offered to pollinators by flowers (Ryder et al., 2019, 2021). Other factors that may also need to be included are under investigation, for example, amino acid compositions of pollen that promote improved colony performance (Moerman et al., 2017; Stabler et al., 2015). Floral traits and flower selection can both be affected by a range of intrinsic and extrinsic (biotic and abiotic) factors, some of which should be considered when developing a recommended list of plants to grow in particular habitats, but nutritional characteristics will remain a fundamental component of decision making (Baude et al., 2011).

Current recommendations highlighting the need to provide diverse ranges of plant species in pollinator habitats offer options for poly-floral diets that overcome nutritional deficiencies of some pollens or nectars and remain valid. However, pollinator diversity has also been shown to benefit when selected keystone floral species (e.g., offering high quality nutrition) are added to non-targeted floral diversity and efficient identification of such species represents a primary research objective (Saunders et al., 2015).

Conclusions

Effective use of urban green spaces such as gardens in pollinator conservation initiatives would be enhanced if quantitative data identifying preferred plant species were available, but most current advice is based on qualitative observations. Flower selection by foragers is known to be affected by the nutritional quality of both pollen and nectar and chemical analysis may offer a more cost-effective approach, particularly if responses to key characteristics are consistent within major groups.

The feeding frequency of Hymenoptera, particularly the social Hymenoptera, was related to the volume of nectar offered by flowers but greater differentiation between plant species occurred when specific nectar sugar characteristics were considered. Relating feeding rate to the volume of the hexose monosaccharides glucose or fructose in nectar, yielded similar correlations in the total Hymenoptera, and particularly the social Hymenoptera (and for the two social genera analyzed individually, *Apis* spp. *Bombus* spp.). More reliable differentiation between plant species was noted, however, when the percentage glucose or fructose content (particularly glucose content) of nectar was investigated, with significant feeding responses recorded in both the social and non-social Hymenoptera.

These observations suggest there is potential for developing a screening technique supporting selection of plant species used in pollinator habitats (particularly those encouraging social and non-social Hymenoptera). Analysis of pollen using standard techniques can establish whether amino acid levels and lipid content meet the minimum required to support individual or colony development (Moerman et al., 2017; Ryder et al., 2021). Establishing the percentage and volume of glucose or fructose (using techniques employed in the current study) can be used to assess the nutritional value of nectar. When refined and verified, these factors may be used in combination to provide quantitative information on the comparative value of different plant species selected for conservation initiatives. Further work to characterize the feeding responses to these nectar characteristics is required, however, alongside foraging activity for pollen resources, before a comprehensive technique can be developed.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Data availability statement

The datasets used and/or analyzed during the current study are stored in the archive of the Centre for Integrated Pest Management, Harper Adams University, and are available from the corresponding author on reasonable request.

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