RELATIONSHIPS BETWEEN NECTAR PRODUCTION AND HONEY BEE PREFERENCE

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Introduction

A 1989 review of research related to the improvement of nectar production in plants by Shuel[26] presents evidence in support of intentional selection of plant genotypes for better nectar production. Such superior genotypes could be of great benefit for both beekeepers and other agricultural producers.

The selection of better nectar-producing plants to improve honey production requires a reliable and efficient system for screening large numbers of candidate plants. Physical measurement of nectar production, using centrifugation[28], capillary tubes[7,21], filter-paper wicks[1], or water extraction[24], is often feasible; but for plants with large numbers of small flowers, estimates of total nectar production can be very labour intensive and may not accurately measure the amount of nectar available to the honey bees.

The authors have been selecting populations of perennial Labiatae for improved nectar production[25,30] and have wanted an efficient method to screen large numbers of variable plant populations. As an alternative to direct measurements of nectar production, one can rank populations on the basis of measurements of honey bee visitation. However, this would be effective only if there were a strong positive correlation between nectar production and bee visitation and if accurate bee counts could be performed more easily than direct nectar measurements.

In preliminary field plots, we found that accurate and repeatable bee counts could be obtained more readily than could sufficient data from direct nectar measurements for *Agastache* spp. and *Pycnanthemum* spp. However, the relationship between nectar production and bee visitation remained to be determined. In preparation for experiments to evaluate this relationship in our test populations, we prepared a literature review that serves as the basis for this report. This review examines published reports that evaluate the relationship between nectar production and honey bee preference among different plant populations.

These reports help to answer some questions about the efficiency of honey bees in judging food resources. But there are factors that can vary among plants tested that could interfere with generalizations about bee efficiency. For instance, although one plant may produce more nectar sugar than another, it could have

flowers shaped to make a bee's feeding more difficult. In such a case, the efficient bee might still choose the plant with less nectar production.

Relationships between nectar production and bee visitation

Forage legumes have been popular experimental organisms for studies of the relationship between nectar production and bee preference because of their agronomic importance and inconsistent seed production. Such studies, however, are often confounded by variation for factors other than nectar production that influence bee visitation, such as ease of tripping[26], aroma[17], corolla tube length[11], and colour[13]. Keeping these limitations in mind, we identified for analysis ten reports of field studies that examine the relationship between nectar production in forage legumes and honey bee visitation.

Table 1 summarizes the results of these ten reports. Seven reports[1, 5, 13, 15, 22, 23, 29] indicate a positive statistical relationship between nectar sugar production or nectar volume and honey bee visitation, with three of these[1, 5, 13] reporting that more than half the observed variability in bee visitation could be accounted for by differences in nectar sugar production. The remaining three reports do not show any statistical relationship. Two[6, 16] failed to collect data to evaluate the role that differences in floral density can play in bee preference, and one[16] was also confounded by significant differences in floral aroma. One should note, however, that the primary purpose of Loper and Waller's study[16] was to measure the influence of floral aroma on bee preference, not to measure whole-plant nectar production. Differences in floral aroma and in ease of tripping may also have contributed to the lack of a statistical relationship in Jabłoński's report[12]. None of these papers reported a significant negative relationship between nectar sugar production and honey bee preference.

There has been great interest in the role that honey bee preference plays in fruit and seed production for plants other than forage legumes. This interest, however, has rarely been expressed in the form of well-designed scientific investigations of the relationship between nectar production and honey bee visitation.

The following paragraphs consider five reports we identified that scientifically test this relationship for plants other than forage legumes. In addition, we found evidence of three other studies suggesting that honey bee visitation is positively correlated with nectar production of *Helianthus annuus* in Hungary[3] and in the USA[8], and of *Vaccinium corymbosum* in the USA[9, 18]. These reports contain statements supporting such a correlation, but present no data for objective analysis and will not be considered further.

Table 2 summarizes the results of five studies of plants other than forage legumes. Three of these studies indicate a positive relationship between nectar production and honey bee visitation[2, 10, 27]. The report by Ayers *et al.*[2] is especially interesting for it is the only study that evaluates selected populations of plants grown exclusively for bees, including *Agastache rugosa*, *Asclepias tuberosa*, *Echinops sphaerocephalus*, *Leonurus cardiaca*, *Nepeta cataria*, *Scrophularia nodosa*, and *Trifolium pratense*. The authors examined plants with great variation in nectar production.

TABLE 1. A summary of field studies examining the relationship between nectar production in forage legumes and honey bee visitation.

Plant species	Citation	Populations evaluated	Year(s) evaluated	Relationship between nectar production & bee preference	Notes
Lotus corniculatus L.	5	6 cultivars	1978–79	Strong positive correlation between total number of flowers in test plot and aggregate bee visitation, r = 0.95**; positive correlations between total number of flowers and bee visitation within varieties, r = 0.74** to 0.94**; no correlations presented to measure bee preference among varieties.	No significant differences in nectar sugar per floret; varietal differences in nectar production based on differences in total number of florets.
Lotus corniculatus L.	22	8 cultivars	1979	Honey bee visitation among cultivars was positively correlated with number of umbels per plant, r = 0.66, and total nectar sugar per plant, r = 0.55.	
Medicago sativa L.	12	15 cultivars	1982–83	Reported no significant correlations in 1982; in 1983, total insect density among cultivars was positively correlated with nectar sugar yield, r = 0.57*.	We tested for a relationship between honey bee densities and nectar sugar yield and found no significant correlations for either year.
Medicago sativa L.	13	26 clones	1965	Field attractiveness of clones to honey bees correlated positively with nectar production, r = 0.77**, and with nectar sugar concentration, r = 0.84**.	

TABLE 1 *Continued*

Plant species	Citation	Populations evaluated	Year(s) evaluated	Relationship between nectar production & bee preference	Notes
Medicago sativa L.	16	7 clones	?	No siginificant correlation between nectar sugar production and honey bee visitation.	Only reported on measurements taken on three days; used cut inflorescences to measure bee preference, eliminating differences in flower number; study was designed to test differences in in floral aroma.
Medicago sativa L.	23	16 clones	1947	Field attractiveness of clones to honey bees was correlated positively with nectar sugar production, r = 0.57*.	
Medicago sativa L.	29	2 selected lines from a single population.	1982–84	Line selected for high nectar volume had over twice the nectar production and over 35% higher honey bee density than the line selected for low nectar volume.	Data on nectar production were taken twice a day for seven days over one, two-week period. Honey bee densities were measured every two hours between 08.00 h and 18.00 h. In a personal communication, L R Teuber reported a correlation of r = 0.50** between nectar sugar and honey bee density.
Onobrychis viciifolia Scop.	15	1 cultivar	1966–68	An F-test was used to show highly significant, positive effects ($P << 0.01$) of nectar volume and nectar sugar concentration on honey bee density.	A single cultivar was evaluated at two sites on 322 occasions over 3 years.

TABLE 1 *Continued*

Plant species	Citation	Populations evaluated	Year(s) evaluated	Relationship between nectar production & bee preference	Notes
Trifolium pratense L.	1	5 strains	1943	Of the five strains tested, the strain 'Corl' was preferred by honey bees and had the highest nectar sugar production and the highest flower density.	We tested for a relationship between honey bee densities and nectar sugar yield among strains and found a highly significant correlation, r = 0.86**.
Trifolium pratense L.	6	8 cultivars	1974	No evident correlation between nectar sugar content or nectar volume per flower and number of insect visits.	There was no report of data on floral density.

*, ** statistical significance at the $P \leq 0.05$ and $P \leq 0.01$ levels, respectively.

The strength of the correlation in their study is particularly high (table 2), suggesting that weaker correlation coefficients in other studies may be associated with less variability in nectar production among plants evaluated. This was clearly evident in Eriksson's study of *Trifolium pratense*[6], in which nectar production varied little among the eight cultivars examined.

Although there were large differences in nectar volume and sugar concentration in nine Labiatae (*Coridothymus capitatus*, *Melissa officinalis*, *Phlomis viscosa*, *Rosmarinus officinalis*, *Salvia fruticosa*, *Salvia hierosolymitana*, *Salvia judaica*, *Satureja thymbra*, and *Stachys aegyptiaca*) evaluated by Dafni et *al.*[4], these differences were not well correlated with bee preference. This may have resulted because the study did not measure the quantity of nectar actually available to honey bees. Four plant species had corolla tubes at least 9 mm long, and these plants were rarely visited by honey bees. Of the five species with shorter corolla tubes, three (*C. capitatus*, *R. officinalis*, and *Stachys aegyptiaca*) showed highly significant correlations between the number of open flowers and honey bee visitation. The authors did not report on the relationship between the number of open flowers and total nectar sugar production, but their data suggest that this would be a worthwhile area for investigation. If one assumes that the nectar volume and sugar concentration of individual flowers of these three species do not vary significantly with flower number, there appears to be a linear relationship between total nectar-sugar production and honey bee visitation.

The only study of plants other than forage legumes that showed no relationship between nectar sugar and bee visitation is that by Mayer *et al.*[20] for *Malus* spp. The cultivars studied had

TABLE 2. A summary of field studies examining the relationship between nectar production and honey bee visitation for plants other than forage legumes.

Plant species	Citation	Populations evaluated	Year(s) evaluated	Relationship between nectar production & bee preference	Notes
Fragaria x *ananassa* Duchesne	27	6 cultivars	1982–84	Strong positive correlation between the number of honey bees working per 1000 flowers and the combined quantity of nectar sugar and pollen in those flowers, r = 0.95 (significance level not reported).	Honey bee densities and pollen and nectar sugar production were also expressed on a per hectare basis. We performed regression analyses on these data and found only a significant correlation between nectar sugar per hectare and bee density among cultivars, r = 0.49*.
Helianthus annuus L.	10	male-fertile and male-sterile lines of 2 varieties	1982	Honey bee densities correlated positively with quantity of nectar secreted, r = 0.08 and 0.88*, and with sucrose concentration, r = 0.76 and 0.62.	There was no report of data on floral density.
Malus spp.	20	39 cultivars	1982–83	Only characteristics of flower colour were significantly correlated with honey bee density and behaviour. No signficant correlations were found between nectar sugar production and honey bee visitation.	There was no report of data on floral density.

TABLE 2 *Continued*

Plant species	Citation	Populations evaluated	Year(s) evaluated	Relationship between nectar production & bee preference	Notes
Nine Labiatae species	4	9 species	1984–85	Strong positive correlation between number of open flowers and honey bee visitation in 1985 for *Coridothymus capitatus* L., r = 0.77**, *Rosmarinus officinalis* L., r = 0.51**, and *Stachys aegyptiaca* Pers., r = 0.71**. No relationship between number of open flowers and total nectar sugar production was established.	Four species had corolla tubes at least 9 mm long. These species were rarely, if at all, visited by honey bees.
Seven different genera	2	8 populations	1986	Strong positive correlation between nectar sugar yields and honey bee visitation for 7 of 8 test populations, r = 0.98**.	Only the globe thistle, *Echinops sphaerocephalus* L., deviated from the observed relationship. This may be due, in part, to the reaction of foraging bees to the unusual morphology of this plant's inflorescence.

*, ** statistical significance at the $P \leq 0.05$ and $P \leq 0.01$ levels, respectively.

white, pink, red, or rose flowers, and visible flower colour and UV reflectance overrode any possible effect of nectar production on bee behaviour. This study supports Mayer's earlier observation[19] that honey bees foraging on white apple blossoms avoid pink and red flowers, which is probably because of the wavelengths of light that bees perceive[14].

Conclusion

Published reports of fifteen field studies investigating possible relationships between nectar production and honey bee visitation were analysed. Ten studies showed a positive relationship between nectar volume or nectar sugar production and bee visitation. Of the remaining five studies, three did not consider the influence of floral density on bee preference[6, 16, 20]. Variation in floral aroma complicated results in studies of *Medicago* by Loper and Waller[16] and of *Helianthus* by Fonta *et al.*[10]. Differences in flower colour were important confounding factors in *Malus*[20] and *Medicago*[16]. And differences in floral morphology strongly influenced the results of Dafni *et al.*[4] for Labiatae.

Researchers wishing to use bee count data to infer differences in nectar production must answer the following questions:

1. Do the plants to be evaluated vary widely in nectar production ? If they do not, any differences observed in bee preference will likely be due to factors other than nectar production. These factors may be less important in no-choice situations than they are in choice tests.
2. Do the plants differ in availability of nectar to honey bees ? Although plants with long corolla tubes may produce large quantities of nectar, other insect visitors may exclude honey bees from these plants.
3. Do some of these plants emit undesirable aromas or display flower colours that bees cannot perceive ? Such variation can confound results.
4. Are bees using these plants primarily for nectar, or is pollen collection important ? If pollen collection is important, bee preference may be more closely related to pollen production than to nectar production.

If these questions can be satisfactorily answered, researchers may be justified in using bee count data as an alternative to direct measurements of nectar production to rank plant populations. Whether or not there is a strict relationship between nectar production and bee visitation, bee count data are an essential part of any programme to select superior bee forage.

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