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Choice of flowers by foraging honey bees (*Apis mellifera*): possible morphological cues

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Abstract. 1. Honey bees foraging for nectar on lavender (*Lavandula stoechas*) chose inflorescences with more of their flowers open. The number of open flowers predicted whether an inflorescence was visited by bees, inspected but rejected, or ignored. Inflorescences chosen arbitrarily by observers had numbers of open flowers intermediate between those of visited and ignored inflorescences.

2. Differences in morphological characters between types of inflorescence correlated with nectar volume and sugar weight per flower so that visited inflorescences had a disproportionately greater volume of nectar and weight of sugar per flower and greater variance in nectar volume.

3. Although there were significant associations between nectar content and the morphological characters of inflorescences, discriminant function analysis revealed discrimination on the basis of morphology rather than nectar content.

4. Visited inflorescences tended to have smaller than average flowers but bees tended to probe the largest flowers on visited inflorescences.

5. Choice of flowers within inflorescences is explicable in terms of the relationship between flower size and nectar content.

Key words. Honey bees, *Apis*, lavender, *Lavandula*, foraging preference, nectar, flower morphology.

Introduction

Foraging worker honey bees (*Apis mellifera* L.) behave like many other predators when seeking nectar from flowers. Although they encounter many potential feeding sites (flowers), they sample only some (e.g. Frankie & Vinson, 1977; Wetherwax, 1986). They thus appear to be choosy about the flowers they visit. Such choosiness is predictable from optimal foraging theory (Stephens & Krebs, 1986) which implies that bees estimate the food value of each flower relative to the cost of exploitation. Several studies have revealed correlations between choice of flower and nectar content among bees (e.g. Marden, 1984; Corbet *et al.*, 1984; Wetherwax, 1986), qualitatively supporting optimal site selection. Other studies, using artificial flowers, have shown close approximation to quantitative models of flower visitation and nectar harvesting (e.g. Waddington & Holden, 1979; Schmid-Hempel *et al.*, 1985; Harder & Real, 1987; Cartar & Dill, 1990).

In this paper we consider the cues that worker honey bees might use in choosing whether to visit and sample a flower. Are there identifiable features that predict nectar content, and do they correlate with the decision by bees to visit or ignore a flower? Cameron (1981), Marden (1984) and Bell *et al.* (1984) suggested that bees could detect the odour of nectar and discriminate on this basis; Wetherwax (1986), on the other hand, concluded that honey bees probably use the odour of previous visiting workers to avoid flowers with depleted nectar content (see recent experimental confirmation in both honey bees (Giurfa & Nunez, 1992) and bumblebees (Schmitt & Bertsch, 1990)). However, such odours are short-lived (Giurfa & Nunez, 1992) and the conclusion that bees use the odour of previous visitors begs the question of how preferences arise initially. Moreover, while the odour of previous foragers might indicate depleted flowers, bees must still choose between flowers that are unmarked. One obvious way is to use the morphological and other physical characteristics of the

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flowers themselves if these correlate reliably with nectar content (Barrow & Pickard, 1984; Galen & Newport, 1987; Harder, 1988). Here, we look at the possible role of morphological characters in the choice of French lavender (*Lavandula stoechas*) flowers by workers of an Italian strain of honey bee in Portugal.

L.stoechas is a xerophytic, aromatic shrub up to 1 m tall that occurs commonly in shrubland communities on the Iberian peninsula (e.g. Herrera, 1991). Plants grow and flower in most populations during late winter and spring and are dormant during summer and autumn (Herrera, 1991). The flowers of *L.stoechas* are hermaphroditic and tubular with a conspicuous, purple corolla and are arranged in a dense inflorescence. Inflorescences may comprise up to 100 flowers (Herrera, 1991) and terminate in several showy, sterile, purple bracts. The flowers secrete small amounts of sugar-rich nectar at their base and are strongly protandrous.

Methods

Observations were made during 10 days in April 1991 in a 16 × 16 m area of shrubland at the Quinta de São Pedro field station, Sobreda de Caparica (longitude 9°11′ west, latitude 38°39′ north), Portugal. *L.stoechas* was the dominant shrub species within the study area and honey bees visited inflorescences regularly. Casual observation suggested that most of the bees came from two hives situated within the Quinta, but it is likely that flowers were also visited by bees from elsewhere.

Bees were observed foraging on *L.stoechas* between 09.00 and 12.00 hours, a period determined by the start of foraging activity and the difficulty of obtaining nectar samples later in the day when flowers had been depleted by harvesting and/or evaporation. Three sets of observations were made:

Choice of inflorescence by bees

We divided inflorescences into three categories according to the bees' response to them.

Visited (V) inflorescences were those on which a bee alighted. In all cases bees that alighted and were left undisturbed, probed one or more flowers with the proboscis before departing. Because we wished to measure nectar availability on such inflorescences, however, bees were gently dislodged before having a chance to probe flowers and remove any nectar (see Wetherwax, 1986).

Rejected (R) inflorescences were those that appeared to be inspected by a bee (one or more flowers were touched with the antennae or legs) but on which the bee did not alight (see also Wetherwax, 1986).

Ignored (I) inflorescences were those that bees approached but at which they did not visibly pause or make any physical contact. We thus assume that bees detected but chose to ignore these inflorescences.

Arbitrary (A) inflorescences – in addition to the three categories of inflorescence determined by the behaviour of bees, we also sampled a number of inflorescences that were chosen arbitrarily by observers (see below).

For each inflorescence, we measured five morphological characters which intuitively might be expected to influence decisions to visit, and recorded two measures of nectar availability and time of day (V, R and I inflorescences only). The morphological characters measured were: (a) the length of the inflorescence from its base to the base of the terminal bracts, (b) the height of the inflorescence base above the ground, (c) the number of terminal bracts, (d) the number of open flowers on the inflorescence, and (e) the total number of flowers on the inflorescence. Having taken these measurements for a given inflorescence, we then sampled the nectar content of its flowers. We measured the volume of nectar in each open flower as the length (mm) of capillary uptake in a 30 mm (1 μl) Camlab disposable microcapillary tube. Individual flowers were removed gently from the inflorescence and nectar extracted from the open posterior end by capillarity aided by gentle squeezing. Nectar concentration in each flower was measured as g sucrose/100 g solution using Bellingham and Stanley hand-held refractometers calibrated between 0–50% and 40–85%. The volume and concentration measures were then used (see Bolten *et al.*, 1979) to calculate the weight (μg) of sugar available to the bee in each flower using Búrquez & Corbet's (1991) equation:

$$\mu\text{g sugar} = (S \times L)/30$$

where $S = 1000 \times (\text{conc}\% \times [0.009224] + \text{conc}\%^2 [0.00005961] + 0.007081)$ and L is the length (mm) of capillary uptake in the microcapillary tube.

The minute volume of nectar in some flowers (see also Wetherwax, 1986; Herrera, 1991) precluded measurement of concentration for every flower, thus reducing sample sizes slightly. Based on the nectar samples, we also noted the number and proportion of flowers on each inflorescence that contained at least some nectar.

Choice of flowers within an inflorescence

Undisturbed bees probed only some of the flowers on V inflorescences before leaving. To see whether morphological characters and nectar content affected such decisions, we first measured some morphological characters to see how well they predicted nectar content and then observed bees to note which flowers they visited and which they ignored.

(a) *Measurements of flowers*. For flowers on arbitrarily chosen inflorescences, we measured corolla length and maximum diameter and nectar volume and concentration. We also recorded other characters that could influence the nectar content of flowers, including the height of the inflorescence above the ground, the length of the inflorescence, air temperature at the inflorescence (measured with a RS Components digital thermometer) and the time of day. In addition, we divided the inflorescences vertically into four equal zones, numbering 1–4 from top to bottom, and classified each flower accordingly.

(b) *Choice of flowers by bees.* When a focal bee alighted, we marked the flowers probed with a small spot of paint to distinguish them from flowers the bee passed over without probing ('ignored' flowers). The same measurements as in (a) above were then made for each of the inflorescences visited.

Results

Choice of inflorescence by bees

Morphological characters. To see whether V, R and I inflorescences could be distinguished on the basis of the morphological characters recorded, we carried out a discriminant function analysis with inflorescence length, height above ground, number of terminal bracts and the number and proportion of flowers that were open as independent variables. The resulting discriminant function was highly significant ($\chi^2 = 25$, d.f. = 10, $P < 0.01$), accounted for 92.3% of the within/between groups variance and yielded the greatest contrast in coefficients between the number of terminal bracts (negative) and the number of open flowers (positive) (Table 1). Group centroids for the different types of inflorescence are shown in Fig. 1. If bees used simple morphological cues, we should predict that not only would group centroids be different, but that they would fall into the rank order V > R > I on these morphological cues. A nonparametric factorial analysis (Meddis, 1984) testing this predicted order was highly significant ($z = 4.39$, $P < 0.001$). (We have deliberately chosen the Meddis test here because, unlike any of its parametric equivalents, it allows *a priori*, directional predictions about differences between treatments to be tested.) As expected, the group centroid for A inflorescences, those selected arbitrarily by observers, was intermediate between those of V and I inflorescences (Fig. 1). Correlating variables with the discriminant function produced a strong significant positive coefficient for number of flowers open ($r = 0.93$, $P < 0.001$) but no significant correlation with any other variable. Of the variables measured, therefore, open flowers on the inflorescence appeared to be the most important determinant of which heads were visited. In keeping with this, Meddis factorial analysis revealed a significant trend in the predicted order of flowers open (V > R > I; $z = 4.90$, $P < 0.001$; see Fig. 2) and a similar significant trend in the proportion of flowers open ($z = 3.01$, $P < 0.01$). There were no significant differences for any other morphological measure.

Table 1. Standardized and unstandardized discriminant function coefficients for the classification of inflorescence types by morphological characteristics (see text).

	Discriminant function coefficients	
Variable	Standardized coefficient	Unstandardized coefficient
Inflorescence length	−0.00308	−0.00068
Height	0.01159	0.00043
No. of bracts	−0.28072	−0.18564
No. of flowers open	0.78020	0.09160
Proportion flowers open	0.37347	1.92796

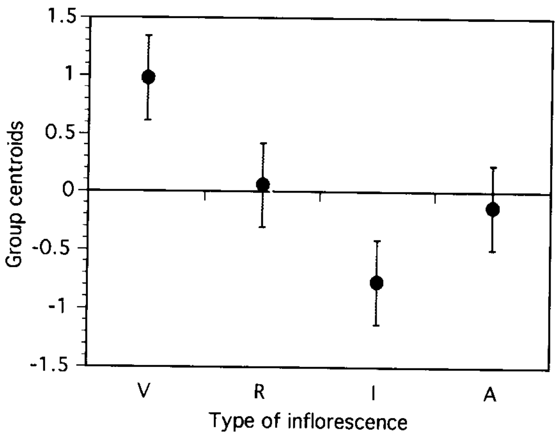

Fig. 1. Group centroids (±standard error) from a discriminant function analysis classifying inflorescence type (see text) by morphology.

Nectar content. Did bias in visitation result in bees gaining more nectar? Clearly, there is likely to be a trivial correlation between the number of flowers open and the total amount of nectar available on an inflorescence. However, since bees usually visited only a small proportion of the open flowers on an inflorescence, preference may have been based on some estimate of relative nectar availability, with flowers on V inflorescences containing more nectar per flower. Such estimates could be based on the amount of sugar available or on less direct indices such as nectar volume or concentration which can in principle vary independently. We therefore tested for differences between inflorescence categories in various measures of nectar availability. Because the availability of nectar is likely to vary with time of day, as a result of both harvesting

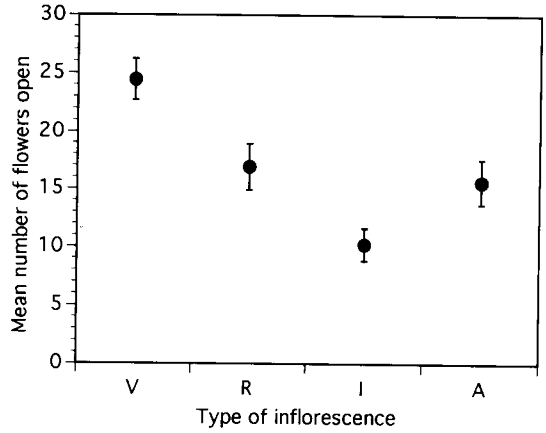

Fig. 2. The mean (±standard error) number of flowers open on each type of inflorescence (see text). Data for eighty-seven inflorescences.

and evaporation (there was a highly significant positive relationship between the temperature at inflorescences and time of day during observation periods (see Methods), $F_{1,207} = 54.57$, $P < 0.0001$) the effect of time (categorized as hourly periods) was taken into account in the analyses.

Inflorescence categories differed significantly in both the mean and standard deviation of nectar volume ($F_{3,76} = 3.23$, $P < 0.05$ and $F_{3,73} = 3.69$, $P < 0.025$ respectively, data $\log_{10}$ transformed to control for association between mean and variance; the use of a single mean value per inflorescence avoids problems of pseudo-replication) with V inflorescences containing more nectar per flower and showing greater variation in nectar volume (Fig. 3a, b). There was a significant negative effect of time of day on both measures ($F_{2,76} = 3.99$, $P < 0.05$ and $F_{2,73} = 3.43$, $P < 0.05$ respectively) but no significant interaction between inflorescence category and time for either measure. Conversely, time of day had a significant positive effect on mean nectar concentration ($F_{3,60} = 3.88$, $P < 0.05$) and a significant negative effect on the proportion of open flowers containing nectar ($F_{3,76} = 3.75$, $P < 0.05$), but there were no significant differences in these measures between inflorescence categories and no significant effect of either time or inflorescence category on the standard deviation of nectar concentration. No significant interaction emerged between time and inflorescence category for either measure of concentration or the proportion of open flowers containing nectar.

Analysis of sugar weights calculated from the volume and concentration of nectar from each flower showed a significant effect of inflorescence category on the mean weight of sugar per flower ($F_{3,56} = 4.14$, $P < 0.05$) with V inflorescences having the highest weights (Fig. 3c), but no significant effect on the standard deviation of sugar weight. Time of day had no significant effect on either measure of sugar weight and there were no significant interactions.

While nectar volume and sugar weight differed significantly between inflorescence categories in the expected direction, it is not clear what aspects of the inflorescences might have predicted them. From the discriminant function analysis of morphological characters, we should expect indices of the number of flowers open to be the best predictors. To test this, we carried out a series of stepwise partial regression analyses with measures of nectar content as dependent variables. The two best morphological predictors of the mean and standard deviation of nectar volume were length of inflorescence and number of open flowers (Table 2). As might be expected, time of day had a significant negative effect on both measures of nectar volume and on the proportion of flowers containing nectar. Also as might be expected, mean nectar concentration increased with time of day, though there was no significant effect on the standard deviation of concentration. There were no significant effects of morphological characters on either measure of nectar concentration. Regression analysis of calculated sugar weights yielded the number of open flowers as the only significant predictor of the mean weight per flower with none of the independent variables predicting the standard deviation of sugar weight.

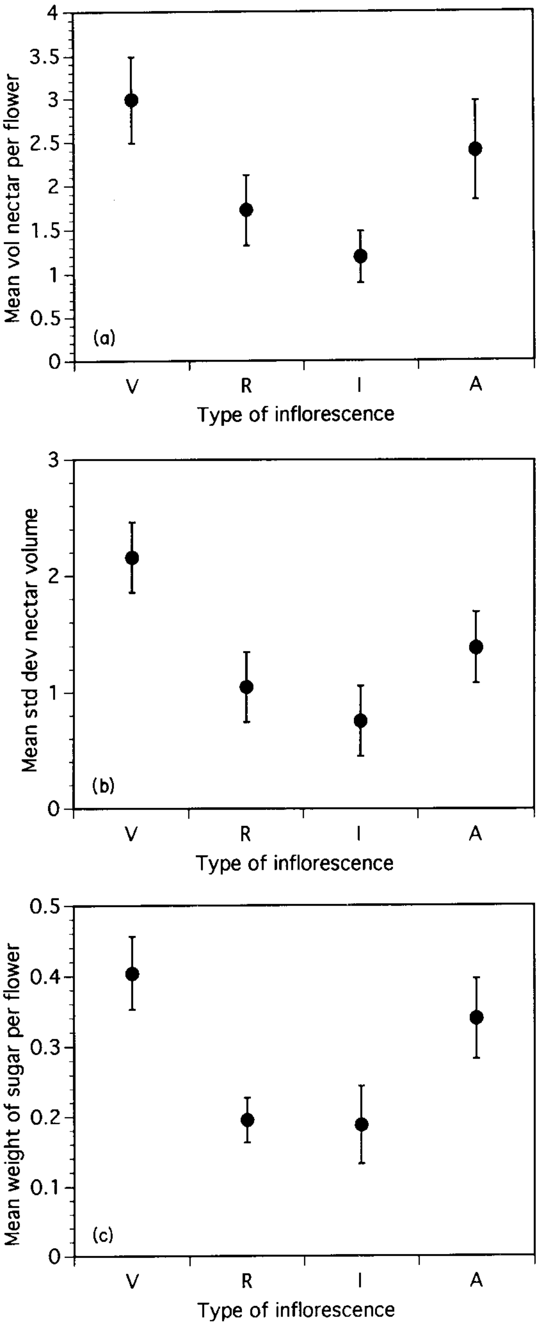

Fig. 3. The mean volume of nectar per flower (μl × 30) (a), the mean standard deviation of nectar volume (μl × 30) (b) and the mean weight of sugar (μg) (c) for each type of inflorescence (see text). Bars represent standard errors.

Overall, therefore, the analysis suggests that the inflorescence characters influencing vists by bees were those indicating nectar content and that bees chose inflorescences on which flowers had a higher than average nectar volume and sugar weight. Although it has been suggested that bees can select flowers by sensing nectar content directly (e.g. Wetherwax, 1986; see also Marden, 1984), a second discriminant function analysis failed to reveal a significant

Table 2. F-ratios from stepwise partial regression analyses of the relationship between measures of nectar content and morphological chatracteristics of inflorescences (see text). $^{*}P < 0.05$, $^{**}P < 0.01$. Minus sign indicates a negative slope.

Dependent variable	Independent variables Length	Height	No. bracts	No. fls open	Ppn fls open	Time	*n*
Mean nectar vol.	2.36*	–	–	2.14*	–	−3.47**	75
SD nectar vol.	2.13*	–	–	3.22**	–	−2.95**	72
Mean nectar conc.	–	–	–	–	–	2.47*	50
SD nectar conc.	–	–	–	–	–	–	50
Ppn fls with nectar	–	–	–	–	–	−2.23*	75
Mean wt sugar	–	–	–	5.77**	–	–	50
SD wt sugar	–	–	–	–	–	–	33

distinction between V, R and I inflorescences on the basis of nectar measures alone. At least at the level of choosing inflorescences, therefore, the results are consistent with bees using morphological cues that correlate with nectar content.

Choice of flowers within inflorescences

Bees usually probed only a small proportion of the flowers on visited inflorescences. If the limited number of probes reflected preference for certain flowers, probed flowers should have had a greater nectar content. We first analysed the relationship between the nectar content of flowers and the morphological and physical environmental measures recorded on arbitrarily chosen inflorescences (see Methods).

Nectar volume, concentration and sugar weight varied inversely with corolla length and, additionally, concentration varied inversely with corolla diameter (Table 3). However, nectar volume and weight of sugar increased significantly with the diameter of the corolla. Nectar concentration was also higher in flowers low on the inflorescence (negative relationship with zone in Table 3) and when the temperature at the inflorescence was high. Overall, therefore, corolla length and diameter were significant predictors of nectar volume and concentration, and thus sugar weight, and in addition concentration, was predicted by the position of the flower on the inflorescence (presumably a function of age) and temperature (presumably due to evaporation).

Our expectation, therefore, would be that bees would preferentially probe the larger diameter flowers within inflorescences but those that were also relatively short. Bees probed flowers with corollas that were both wider ($F_{1,207} = 3.73$, $0.05 < P < 0.1$, Fig. 4a) and longer ($F_{1,207} = 13.21$, $P < 0.001$, Fig. 4b) than flowers that were passed over. Two points are worth mentioning here, however. First, there was a significant positive association between corolla diameter and length ($r = 0.20$, d.f. $= 270$, $P < 0.001$) (see also Galen *et al.*, 1987), so choice based on one character is likely to produce a similar size-bias in the other. Secondly, a separate analysis of corolla length and diameter on V, R and I inflorescences showed a significant effect of inflorescence category on both length ($F_{2,108} = 48.63$, $P < 0.001$) and diameter ($F_{2,108} = 6.18$, $P < 0.01$) with both being smallest on V inflorescences (Fig. 5a, b). Bees thus appeared to choose inflorescences on which flowers were smaller than average, bearing out the negative relationship between nectar and sugar measures and corolla length (Table 3), but within these inflorescences to choose the larger flowers. Possible reasons for this apparent contradiction are discussed below.

Discussion

The results suggest that honey bees chose between inflorescences, and between flowers within inflorescences, on the basis of cues related to nectar content. However, the cues used to choose inflorescences appeared to be different from those used to choose flowers within inflorescences. The results imply that choice of inflorescence is little influenced by floral characters, but depends instead on

Table 3. F-ratios from stepwise partial regression analyses of the relationship between measures of nectar content and the morphological characteristics of flowers on visited inflorescences and other measures that are likely to influence nectar availability (see text). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Minus signs indicate a negative slope.

Dependent variable	Independent variables Length	Diameter	Height	Length	Temp.	Time	Zone	*n*
Nectar volume	−5.49**	3.80**	–	–	–	–	–	272
Nectar conc.	−3.41**	−2.67**	–	–	6.09***	–	−3.89**	80
Wt sugar	−2.78**	2.27**	–	–	–	–	–	80

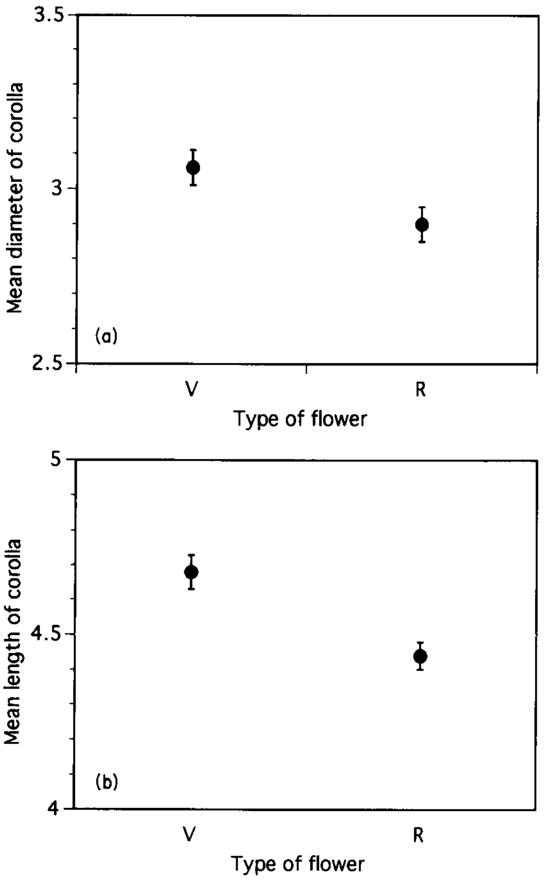

Fig. 4. The mean (±standard error) diameter (mm) (a) and length (mm) (b) of the corolla of flowers that were probed (V) or passed over (R) by bees (see text).

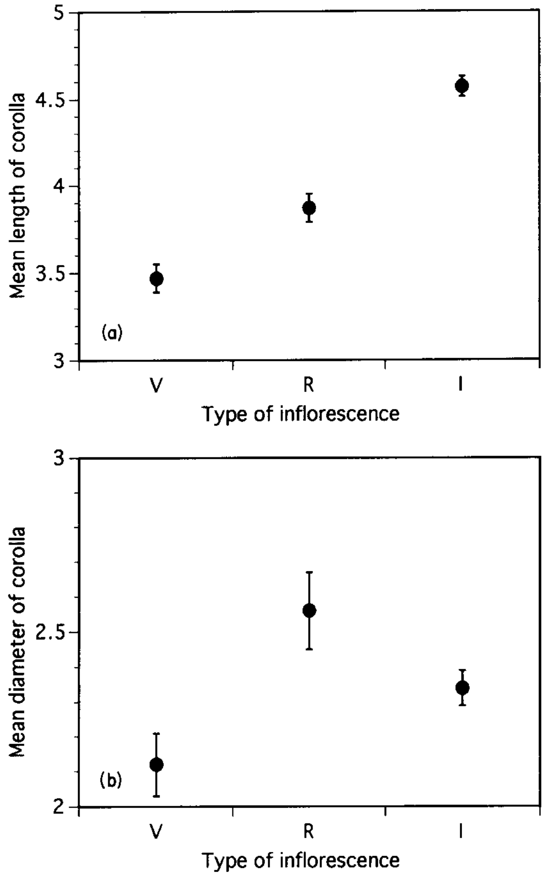

Fig. 5. The mean (±standard error) length (mm) (a) and diameter (mm) (b) of corollas on each type of inflorescence (see text).

the number of open flowers. Once an inflorescence has been chosen, the more rewarding flowers within that inflorescence are chosen on the basis of floral characters.

Visited inflorescences had more open flowers than those that bees rejected or ignored or those sampled arbitrarily by observers. They also tended to have a greater number of showy terminal bracts. The number of flowers open and the length of the inflorescence were significant predictors of nectar volume so that visited inflorescences tended to have a disproportionately greater volume of nectar per flower and greater variance in nectar volume. While we did not investigate it here, the association between mean and variance in nectar volume across inflorescences is interesting in the context of variance-discounting models of risk-sensitive foraging supported elsewhere in nectar-feeding insects (e.g. Waddington *et al.*, 1981; Real *et al.*, 1982). Although there were significant associations between nectar content and the morphological cues distinguishing different categories of inflorescence, discriminant function analysis revealed a significant discrimination on the basis of morphology rather than nectar content. Overall, therefore, the results suggest that visual conspicuousness rather than direct or indirect perception of nectar availability was important in choice of inflorescence. Although scent-marking of visited flowers by bees (Giurfa & Nunez, 1992; see also Schmitt & Bertsch, 1990, for bumblebees) could bias visits to high nectar-content flowers, it did not appear to be important here.

Having alighted on an inflorescence, bees also appeared to be choosy about the flowers they probed, probing wider flowers that were also relatively short. Although bees visited inflorescences with smaller flowers, within these inflorescences they chose the larger flowers. We offer three explanations for this seeming contradiction. First, a flower's dimensions may affect the availability of nectar to bees, with nectar being harder to extract from long, thin flowers compared with shorter, wider flowers, because of more rapid evaporation and increased viscosity (cf. Corbet *et al.*, 1979). Although studies of bumblebees have suggested that nectar is more dilute in flowers with longer corollas (Barrow & Pickard, 1984), the independent effects of corolla width and length on foraging preferences were not analysed. Second, there is often a positive intraspecific correlation between nectar production rates and flower or inflorescence size (Harder & Cruzan, 1990). The complex relationship between rate of nectar production, bee visitation rates and standing crops will determine the correlation between flower and inflorescence size and the standing crop of nectar. However, suitable manipulation experiments could unravel cause-and-effect relationships here. Third, because of the relationship between proboscis length and the efficiency of nectar extraction (Barrow & Pickard, 1984; Harder, 1986, 1988), the structure and dimensions of the bee's proboscis may constrain the size of flower that can be probed effectively, with very small flowers being difficult to harvest, so that within small-flowered heads, bees tend to go for larger flowers in which nectar is more accessible.

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